Assessing the Ecological Importance of Unburned Islands in the Conservation and Management of Wildlife Species: a Case Study on Greater Sage-Grouse Populations in the Sagebrush Ecosystems of South-Eastern Oregon

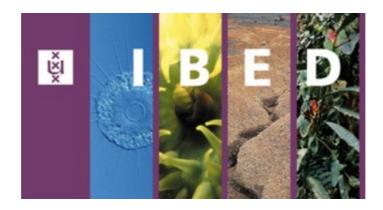
BY

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Abstract

In many ecosystems around the world, fire is a common and often critical component of ecosystem functioning which has been structuring the distribution of ecosystems and their wildlife species for millions of years. Nevertheless, survival of many wildlife species in fire-prone ecosystems has come under increasing pressures, predominately due to alterations in fire regimes caused by climate change and anthropogenic activity. As the ability of wildlife species to cope with fire disturbances depends on their ecological requirements and life history traits, present day fire-impacts may potentially be larger than during a species' evolutionary history. However, as fire is inherently a heterogeneous disturbance, specific components of the landscape may remain unharmed after fire. These areas may mitigate the negative effects of fire disturbances on the survival and persistence of wildlife species by providing habitat in which these species can survive or persist. These refugia, or unburned islands, may be of high importance for wildlife species, yet they remain poorly understood.

To assess the ecological importance of unburned islands in the conservation and management of wildlife populations, the species of interest in this study was the greater sage-grouse. This large gallinaceous bird is a sagebrush obligate species that inhabits the sagebrush ecosystems of the Great Basin of North America. Several life-history characteristics and ecological requirements of sage-grouse make this species interesting in studying the effect of unburned islands on the post-fire dynamics of wildlife species. First, sage-grouse exhibit high philopatry to natal lek sites (mating areas), and second, have high requirements of intact and widespread sagebrush ecosystems. For these reasons, fire may heavily impact sage-grouse populations, whereas unburned islands may potentially completely mitigate the negative effects of fire disturbances.

In this study the post-fire response of sage-grouse lek populations was assessed in relation to the location of their respective lek sites using a long-term unburned islands database. Afterwards, the habitat surrounding the lek sites of these lek populations was modelled at three scales known to affect habitat selection of sage-grouse (0.8km, 6.4km and 18km). Habitat suitability analyses were performed to examine the effect of post-fire habitat composition on the dynamics of these populations. These analyses showed that sage-grouse lek populations are negatively affected by fire if their lek site is situated inside of the burn perimeter. Conversely, it was observed that the opposite applies for lek populations inside unburned islands and outside of the fire perimeter. In these cases, populations are not negatively affected after fire and can even increase in some cases. Furthermore, the results of this research show that the post-fire habitat composition surrounding these respective lek sites has a strong effect on the population dynamics after fire. Habitat surrounding lek sites that had a higher proportion of suitable vegetation types at the small-scale (0.8km) and contained lower proportion of unsuitable cheatgrass cover and higher proportion of suitable vegetation height at the 6.4km scale resulted in better population responses after fire. On a 0.8km scale, lek sites inside of unburned islands had a significantly higher amount of unburned area, percentage area with suitable vegetation types and vegetation height than lek sites inside the fire perimeter. At the 6.4km and 18km scale, unburned island lek sites had less cheatgrass cover than fire perimeter lek sites. These characteristics may explain why unburned island lek populations respond better to fire disturbances than fire perimeter lek populations. The results

of this study also indicate that on a small-scale, residual patches of suitable vegetation may act as wildfire refugia for sage-grouse lek populations, allowing for their post-fire persistence.

These results are important findings for the long-term management of sage-grouse populations in the Great Basin. The results show that construction and preservation of unburned patches of vegetation surrounding lek sites in an increasingly burned landscape may potentially allow for the long-term persistence of sage-grouse populations. Furthermore, the results of this research increase general understanding of the ecological function of unburned islands for wildlife species by showing the potential of unburned islands to allow for the post-fire persistence of a high philopatry species like the greater sage-grouse. Such information may be used to try and understand the effects of unburned islands on the post-fire dynamics of other wildlife species in both sagebrush and other fire-prone ecosystems around the world.

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1. Introduction

In many ecosystems around the world, fire is a common and often critical component of terrestrial ecosystem functioning (Flannigan et al., 2009). Fire has been structuring the distribution of ecosystems and their wildlife species for millions of years (Bond et al., 2005). Nevertheless, the survival of many of these species is under increasing pressure from global environmental change, including alterations in fire regimes caused by climate change and anthropogenic activity (Flannigan et al., 2009; Murphy et al., 2013). The ability of wildlife species to cope with fire disturbances highly depends on their ecological requirements and life-history attributes (Sousa, 1984), and for this reason, present-day fire impacts on wildlife species are potentially greater than those experienced by species during their evolutionary history (Brook et al., 2008). However, because fire is inherently a heterogeneous disturbance, specific components of the landscape may endure after fire (Burton et al., 2008). These areas may mitigate the negative impacts of fire disturbances on wildlife species by providing habitat in which they can survive and from which they can repopulate, increasing their likelihood of survival or persistence (Turner et al., 1997; DeLong and Kessler, 2000; Robinson et al., 2013). Therefore, these so called fire refugia, or unburned islands, may be of high ecological importance in the conservation and management of wildlife populations during and after fire. Yet, refugia presently remain poorly understood (Kolden et al., 2012; Robinson et al., 2013).

In the sagebrush ecosystems of the Great Basin of North America, fire is also becoming an increasingly bigger threat to wildlife species, predominantly because of fire regime alterations through the invasion of exotic grasses like cheatgrass (*Bromus tectorum*) and trees like juniper (*Juniperus occidentalis*), as well as climate change and human activity (Connelly et al., 2004; Westerling et al., 2006). These phenomena have resulted in a higher frequency and intensity of fires which may now rapidly reach catastrophic sizes of larger than 100.000ha, with detrimental effects on ecosystem health (Miller and Eddleman, 2000; Miller et al., 2011). Even at low intensity, wildfire in sagebrush ecosystems often burns all stands of vegetation (Baker, 2006). Furthermore, effects of fire on wildlife are long-term as sagebrush requires between 20-50 years to recover (Connelly et al., 2000; Nelle et al., 2000; Lesica et al., 2007).

Despite this, most fires in sagebrush ecosystems burn in a heterogeneous pattern and leave a mosaic of both burned areas and unburned islands of vegetation (Boltz, 1994). Unburned islands might be crucial for population recovery of wildlife species because they might serve as refugia during and after fire (Foster, 2016). However, climate change induced alterations in fire activity may lead to a reduction in these unburned islands (Abatzoglou and Williams, Meddens et al., 2018). For these reasons, natural resource managers in the Great Basin are increasingly interested in identifying and understanding the role of unburned islands for preserving species and ecological functions of ecosystems (Meddens et al., 2017b).

To assess the ecological importance of unburned islands in the conservation of wildlife species, the species of main interest in this study is the greater sage-grouse (*Centrocercus urophasianus*: hereafter: sage-grouse), a sagebrush obligate bird which inhabits the sagebrush ecosystems of the Great Basin. This species is still widely distributed throughout its range, but its populations have declined by approximately half over the last century, partially due to habitat degradation by fire disturbances (Schroeder et al., 2004,

Garton et al., 2011). Although the specific effect of wildfire on sage-grouse population dynamics and habitat selection remains largely unknown (Foster, 2016), the well-known life history characteristics and ecological requirements of sage-grouse may give some indication about how populations of this species respond to fire disturbances (Crawford et al., 2004; Connelly et al., 2011b), as well as to why unburned islands may be important to their long-term population persistence.

First, sage-grouse exhibit strong site fidelity to home and seasonal ranges, where individuals typically return to the same lek (mating site) or groups of leks on a yearly basis (Wallestad and Schladweiler, 1974; Dunn and Braun, 1985). For example, female sage-grouse tend to place their nests in close proximity (< 200m) to previous year's nests (Gates, 1983). Due to this high philopatry, sage-grouse may remain in fire disturbed habitat and attempt to select habitat at the micro-scale to meet their requirements, even if it has severe fitness costs (Rettie and Messier, 2000, Foster, 2016). Second, sage-grouse are true sagebrush obligates, and require widespread and intact sagebrush habitat during all stages of their life, as well as for food and cover from predators (Patterson, 1952; Crawford et al., 2004; Hagen, 2011b). Suitable sagebrush habitat and extent are therefore directly linked to nesting success and survival of this species (Wallestad and Pyrah, 1974; Gregg et al, 1994; Connelly et al., 2011a). Sage-grouse select nest and brood-rearing sites based on specific micro-scale vegetation characteristics (Connelly et al., 2011a; Schreiber et al., 2015). This predominantly involves sagebrush and grasses (Wallestad and Eng, 1975; Drut et al., 1994a), where nesting and breeding sage-grouse preferably utilize areas with larger and more densely covered stands of vegetation (Wakkinen, 1990; Sveum et al., 1998), as well as placing nests under the tallest stands of vegetation available at a particular site (Wallestad and Pyrah, 1974; Wakkinen, 1990). Additionally, sage-grouse essentially avoid areas that are invaded by cheatgrass as it offers inadequate nesting cover and these areas are often highly disturbed (Crawford et al., 2004; Knick et al., 2013). Furthermore, sage-grouse distribute their nests in relation to the proximity of mesic resources used during brood-rearing season (Donnelly et al., 2016). Because of these life history characteristics and requirements, observed declines in sagegrouse populations following wildfire are most likely caused by reduced survival and reproduction, rather than due to emigration of sage-grouse away from fire-affected areas (Coates et al., 2015). Accordingly, suitable post-fire habitat characteristics and unburned islands may be important in determining the response of sage-grouse populations to fire.

For these reasons, the aim of this research was to utilize information from a long-term unburned island database by Meddens et al. (2016) to increase understanding of the effect of unburned islands within the fire perimeter on post-fire dynamics and persistence of sage-grouse lek populations in the sagebrush ecosystems of the Great Basin. In this research, a lek population refers to the population of individual male-sage grouse inhabiting the range around a specific lek site. The fire perimeter is the entire length of the outer edge of the fire.

Assessing the importance of unburned islands for wildlife species is a key issue, as there are major knowledge gaps relating to the spatial patterns and dynamics of wildlife populations within post-fire vegetation mosaics (Robertson et al., 2013). Increased knowledge about this topic could assist in conservation and management of fire-sensitive species like the sage-grouse by determining whether management through protection and construction of unburned islands may allow for their long-term persistence in an increasingly burned

landscape in the future. To accomplish this, the pre- and post-fire dynamics of sage-grouse lek populations were first assessed in relation to their spatial distribution surrounding past fires to gain insights into the effects of fire and unburned islands on sage-grouse population trends. Afterwards, the post-fire habitat composition surrounding these lek sites was modelled deductively at multiple spatial scales (0.8km, 6.4km and 18km), because spatial scale might affect habitat selection patterns of sage-grouse lek populations. Habitat modelling was performed to find out if and at which scales, the post-fire habitat characteristics surrounding lek sites affects dynamics of sage-grouse lek populations after fire disturbance.

1.1 Hypotheses

Based on available literature about the life-history characteristics, ecological requirements and dynamics of sage-grouse populations to fire, this research has the following two hypotheses:

1. Fire has a negative effect on the post-fire population trend of sage-grouse lek populations if their respective lek site is located inside the fire perimeter, whereas lek populations with lek sites inside of unburned islands or outside of the fire perimeter are not negatively affected by fire.

Post-fire declines of sage-grouse lek populations in the fire perimeter are hypothesized because of the high philopatry of sage-grouse to natal lek sites (Wallestad and Schladweiler, 1974; Dunn and Braun, 1985), the strict requirements of sage-grouse of intact and widespread sagebrush vegetation (Crawford et al., 2004; Connelly et al., 2011b) and the long-term (20-50 years) degradation of sagebrush after fire (Nelle et al., 2000; Lesica et al., 2007). Consequently, loss of sagebrush surrounding lek sites, which is used for nesting, breeding, cover and food (Crawford et al., 2004), may have long-term negative effects on sage-grouse survival and reproduction (Coates et al., 2015). Evidence of these characteristics is supported by research from Foster (2016), who found that individual sage-grouse continued to utilize fire disturbed habitat surrounding lek sites, which had severe fitness costs in at least the first years after fire. Furthermore, due to loss of adequate habitat, post-fire nesting success in the burned landscape was amongst the lowest reported for sage-grouse (Foster, 2016).

In contrast to fire perimeter lek populations, it is hypothesized that wildfire effects on unburned island lek populations is mitigated because these areas may function as wildfire refugia by preserving key habitat functioning (Robinson et al., 2013). For instance, unburned islands continue to provide cover from predation, as well as providing a direct food source, which both positively affect post-fire nesting success and survival of sage-grouse individuals (Wallestad and Pyrah 1974; Gregg et al., 1994). Sage-grouse may utilize these unburned islands to persist and recover from fire during the years in which the surrounding burned landscape recovers to its pre-fire conditions.

2. An increase in the proportion of suitable post-fire habitat surrounding lek sites is positively related to the recovery and persistence of their respective sage-grouse lek populations after fire.

Sage-grouse are true sagebrush obligates, and require intact and widespread sagebrush during all stages of their life (Patterson, 1952; Crawford et al., 2004). Consequently, it is hypothesized for several reasons that an increase in the proportion of suitable post-fire habitat for sage-grouse surrounding their respective lek sites improves their long-term lek population response to fire. In general, larger patches of unburned islands are of higher ecological value than smaller unburned island, because larger unburned islands have the potential to harbour more plant and animal species and have a higher diversity in natural resources. Furthermore, larger unburned islands allow for safer dispersal (Longland and Bateman, 2002). Second, the extent of suitable sagebrush cover and height are positively related to nest use and nesting success (Wallestad and Pyrah, 1974; Gregg et al., 1994), largely because they reduce predation by birds of prey (DeLong et al., 1995; Hagen, 2011b). Moreover, specifically during winter when snow may completely cover short sagebrush stands, sage-grouse rely almost exclusively on large sagebrush exposed above snow for food (Connelly et al., 2000; Connelly et al., 2004). Lastly, sage-grouse avoid areas invaded by cheatgrass, as these offer an inadequate source of food and cover and are often related to human and natural disturbances (Crawford et al., 2004; Knick et al., 2013). These characteristics show that an increase in proportion of suitable habitat may enhance post-fire population response of sagegrouse to fire.

1.2 Background

In the following paragraphs, a detailed explanation will be given on the history of wildfire in the sagebrush ecosystems of the Great Basin and the present dynamics of wildfire activity in this region. Thereafter, the ecological implications of wildfire for sagebrush ecosystems and sage-grouse will be discussed. Lastly, the importance of unburned islands in sagebrush ecosystem dynamics and the potential of remote sensing techniques in wildfire management are examined. A summary of the theoretical framework, including the most relevant interactions for sage-grouse conservation in the sagebrush ecosystems of the Great Basin, can be seen as a conceptual diagram in Figure 3.

The History of Wildfire in Sagebrush Ecosystems

In the Great Basin, wildfires are a common and often a critical component of terrestrial ecosystem functioning (Flannigan et al., 2009; Miller et al., 2013). The ecological properties and species distribution in the Great Basin are largely influenced by its fire regime (Bond et al., 2005). Wildfires reshape the landscape by providing new physical and biological properties and micro-climatic conditions for plant and associated animal species through release of nutrients and moisture and increased light availability. This process may maintain or restore native plant composition and structure or result in the emergence of new plant communities (Ellsworth and Kauffman, 2017). Consequently, additional habitat complexity is created due to higher spatial heterogeneity (Swanson et al., 2011).

Sagebrush (*Artemisia tridentata*) and its subspecies are a dominant component of the Great Basin's vegetation communities (Chambers et al., 2007). Sagebrush ecosystems are defined as ecosystems where one or more sagebrush taxa dominate the vegetation of the landscape. Prior to Euro-American settlement, fire-return intervals in these sagebrush ecosystems were between approximately 15 to 110 years (Whisenant, 1990; Miller and Rose,

1995; Heyerdahl et al., 2006), depending on prevailing natural conditions such as fuel availability, location of lightning strikes, climate and weather (Westerling et al., 2003). Historically, fire-free intervals were shorter on more productive sites for plant growth and higher elevated landscapes as compared to less productive and lower elevated landscapes, indicating the importance of fuel availability and continuity in determining fire frequency (Keane et al., 2008). Sagebrush is intolerant to fire and has long recolonization and recovery times of between 20-50 years due to slow seed dissemination and frequent seed mortality after fire (Murphy et al., 2013; Miller et al., 2013). Large fires in sagebrush ecosystems are therefore often extremely impactful (see Figure 1).

Because of their sensitivity to fire, short-term recovery of sagebrush ecosystems after large fires depends on seedling establishment from unburned seeds in the seed bank or short-range dispersal from unburned islands (Keane et al., 2008). Sagebrush was able to evolve with and recover from periodic fire in the past because fuel continuity was frequently insufficient to carry large surface fires, giving time for pre-burn abundance to recur (Akinsoji, 1988; Abatzoglou and Kolden, 2011; Ellsworth and Kauffman, 2017).



Figure 1: Impact of fire on the sagebrush ecosystems of south-eastern Oregon. Left is before and right is after fire. Imagery retrieved from Bureau of Land Management and Davies et al. (2014).

Present Dynamics in Wildfire Activity

Recently, fire regimes in sagebrush ecosystems have changed significantly as a result of climate change (Westerling et al., 2006; Flannigan et al., 2009), invasive annual grass species (Brooks et al., 2004), fire suppression (Murphy et al., 2013), urbanization (Keeley et al., 1999) and other management practices such as grazing (Miller and Eddleman, 2000). Two major shifts have occurred because of these alterations in the fire regime of sagebrush ecosystems: an increase and a decrease in fire frequency (Davis et al., 2011).

First, fire suppression and grazing have allowed woody conifer species such as juniper (*Juniperus occidentalis*) to expand and encroach in mid to high elevation areas (Miller and Rose, 1999; Miller and Eddleman, 2000). Livestock grazing can significantly influence fire by reducing fuel loads through changes in abundance, structure and composition of vegetation. Initially, this led to a reduction in fire frequency and size because of the reduction in fuel continuity (Chambers et al., 2014). However, in combination with continued heavy grazing, this leads to a reduction in native perennial grasses, forbs and shrubs, allowing tree species to reach maturity. On-going infilling of trees results in a change in fuel characteristics and a fire

regime that creates large and severe fires with detrimental effects on ecosystem health (Miller et al., 2011; Miller et al., 2013).

Second, invasion by exotic annuals has led to a remarkable increase in both frequency and size of wildfires (Chambers et al., 2007; Abatzoglou and Kolden, 2011). The invasion of cheatgrass (*Bromus tectorum*), a fast growing annual grass species, has especially changed the mean fire return interval to well below 10 years in many sagebrush communities due to increases in fine fuels (Whisenant, 1990). Higher frequency fires allow cheatgrass to replace the native shrub and herb layers and prevent reestablishment of the slow growing sagebrush communities, leading to monocultures of invasive annual grasses (Crawford et al., 2004; Davis et al., 2011; Brooks et al., 2015). These dynamics result in a positive feedback cycle coined the "grass/fire cycle" by D'Antonio and Vitousek (1992), which facilitates the spread and dominance of invasive annual grasses, promoting even more frequent fire and potentially perpetuating invasive dominance (Coates et al., 2016).

Lastly, climate change scenarios for sagebrush ecosystems predict increasing trends in temperature, frequency of extreme weather and altering seasonality of precipitation (Miller et al., 2011; Flannigan et al., 2009). This is projected to cause widespread increases in fire activity, including total burned area, high severity fires and length of fire-season (Westerling et al., 2006; Abatzoglou and Williams, 2016). Changing climate in the form of increasing temperature and CO₂ concentrations may also affect the spatial distribution of land that is at risk of invasive species by creating new terrain which is climatically suitable for invasions, as well as causing increased competitiveness in plant invaders (Bradley, 2008). For example, research has suggested that increasing CO₂ concentrations increase cheatgrass productivity and fuel load, subsequently altering fire regimes (Ziska et al., 2005).

Ecological Implications of Changing Fire Regimes on Sagebrush and Sage-Grouse

Both shifts in fire regime in the Great Basin have led to a rapid and continuous loss of sagebrush ecosystem, which in turn negatively affects the habitat of many species that require this ecosystem to survive, such as the greater sage-grouse (Brooks et al., 2004). This makes conservation of sagebrush ecosystems one of the most difficult and crucial concerns in western North America (Dahlgren et al., 2015).

Greater sage-grouse, a large gallinaceous bird, historically inhabited big portions of the sagebrush-dominated Great Basin (Coates et al., 2016). Sage-grouse are true sagebrush obligates, and, throughout their lifecycle, require widespread and intact sagebrush landscapes for cover, food, breeding, nesting, brood-rearing and wintering (Crawford et al., 2004). Sage-grouse breeding habitats, such as leks (mating sites) and nesting and brood-rearing sites typically consist of large, relatively continuous stands of sagebrush with patches of open areas containing less herbaceous and shrub cover than the surrounding areas (Connelly et al., 2004). Sage-grouse populations thrive best in situations where more than 65% of the landscape is covered in sagebrush and have difficulty surviving when sagebrush cover is lower than 25%, because habitat requirements in the form of nesting areas, food sources and cover from predators cannot be met (Chambers et al., 2014). During winter, sage-grouse rely almost exclusively on large sagebrush exposed above snow for foraging and cover, indicating the importance of healthy and mature sagebrush in determining suitable habitat (Connelly et al., 2004). Besides sagebrush cover, sage-grouse population dynamics are strongly linked to the

presence of mesic habitats, such as wet meadows, riparian areas and temporary wetlands (Donnelly et al., 2016). Despite encompassing only about 2.4% of the total land area in the Great Basin, mesic sites are important in determining sage-grouse breeding habitat, where population abundance in lek areas increases with proximity to mesic resources (Donnelly et al., 2016).

Due to these distinct ecological requirements, sage-grouse population dynamics are used as a key indicator for the health and extent of sagebrush ecosystems across the Great Basin (Rowland et al., 2006; Chambers et al., 2014). Loss of sagebrush ecosystems due to wildfires and encroaching conifers and annual grasses has serious negative impacts on sage-grouse populations. Consequently, sage grouse populations have presently declined to approximately 50% of their original range (Schroeder et al., 2004). For instance, it was found that leks were inactive when as little as 4% of the landscape was covered in conifer trees. Active leks disappear when conifers were uniformly spread throughout the landscape as compared to being clumped, indicating the importance of spatial patterns in disturbances on sage-grouse behaviour (Baruch-Mordo et al., 2013). In addition to their influence through spatial composition, conifer trees alter soil acidity, shade out other native plants, compete for water and nutrients and serve as perches and roosts for birds that prey on sage grouse eggs and nestlings. This eventually leads to a reduction in food and cover for sage grouse and other fauna (Miller et al., 2005).

In the face of climate change, loss of sagebrush ecosystems and sage-grouse habitat will most likely be amplified. Intensified droughts may worsen wildfire activity and loss of sagebrush ecosystem (Westerling et al., 2006), while also decreasing the abundance of and increasing the distance to mesic resources necessary for sage-grouse foraging (Donnelly et al., 2016). Sagebrush ecosystems that are burned and invaded by cheatgrass enter an alternate fire regime, heightening vulnerability for future burning, which destroys even more sage-grouse habitat (Balch et al., 2013). Warmer and drier climatic conditions may also favour the expansion of invasive species into areas that were previously too cool and moist, such as high elevation sagebrush ecosystems in the case of cheatgrass (Bradley, 2008; Chambers et al., 2014).

Because of these dynamics, restoration of sagebrush communities and their associated fauna may require management in a way that reverts the aforementioned changes caused over the last century, such as controlling fuel conditions, native and invasive plant communities, fire regimes and other ecosystem properties (Brooks et al., 2004). Achieving meaningful long term change within sagebrush ecosystems may ultimately be a result of the ability to identify, prevent and revert the unwanted vegetation shifts caused by wildfires and invasive grass encroachment (Davies et al., 2011).

Unburned Islands and Their Ecological Importance

Unburned islands may be important in the restoration of sagebrush ecosystems and sage-grouse habitat, but have not widely been addressed. Unburned islands are created when fire burns heterogeneously through the landscape, resulting in patches of surviving vegetation within a wildfire perimeter (Meddens et al., 2016). Unburned islands provide habitat for a variety of plant and animal species to which they can retreat to during fire and repopulate burned areas from after fire. Consequently, they may function as wildfire refugia with

important ecological functions for fire subject ecosystems (Turner et al., 1997; DeLong and Kessler, 2000). Two examples of unburned islands in sagebrush ecosystems can be seen in Figure 2.

Refugia like unburned islands were initially defined as components of ecosystems that may facilitate the persistence of plant and animal species during long-term climatic change, but more recently, are also described and studied in the context of shorter time scales where they are created by phenomena such as wildfires (Keppel et al., 2012; Keppel et al., 2015). Unburned islands are created through fire behaviour patterns driven by weather, topography and fuel, where meaningful changes in any of these three components can either form or prevent unburned islands from forming. For example, a transition from flammable vegetation (e.g dry grass) to non-flammable vegetation (e.g riparian vegetation) may promote the formation of refugia (Meddens et al., 2017a).

The characteristics of unburned islands within fire perimeters, such as area, shape, frequency, complexity, topographical and environmental conditions and their relation to surrounding burned and unburned ecosystems constitute critical components of wildfire regimes and are becoming increasingly important in conservation planning (Keppel et al., 2015). To understand what role they play in ecosystem dynamics, succession processes and wildfire risk, it is necessary to quantify their characteristics at landscape scale. Most studies, however, have erroneously ignored and excluded unburned islands from fire regime descriptions and research, assuming a uniform burn scar in the landscape. As a result, the characteristics of unburned islands and their large-scale ecological importance remain largely unknown to date (Kolden et al., 2012).

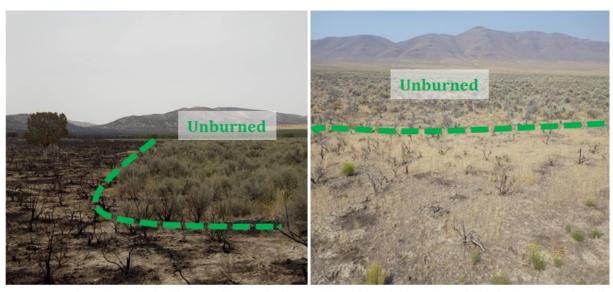


Figure 2: (Left): Unburned Island in Wyoming Sagebrush Stands in Idaho, (Right): Unburned islands of Low Sagebrush in Wyoming. Pictures from Jones et al. (2015) (Left) and https://farm8.staticflickr.com/ (Right), see also References.

The Role of Remote Sensing Applications in Wildfire Management

Since the early 20th century, land management applications like mapping and measuring of wildfire perimeters and burned areas have greatly improved due to major advances in the use of Geographic Information Systems (GIS) and spatial analysis of remote sensed data (Kolden & Weisberg, 2007). The two main federal wildfire databases in the US define burned area as the calculated area within a perimeter, mapped either by Global Positioning Systems (GPS) or

by classification and digitization of a polygon perimeter from satellite data. These methods, however, assume homogeneity in fuel consumption within the fire perimeter, excluding heterogeneous burn patterns and the presence and significance of unburned islands (Kolden et al., 2012).

Although the importance of unburned islands within fire perimeters has widely been addressed in studies of fire effects on ecosystems, their size and patterns have to-date not been included in fire regime descriptions and have not been analysed quantitatively. One of the main reasons for this is that fire perimeter mapping has historically been performed for the purposes of calculating area burned, monitoring containment during suppression and for requesting post-fire rehabilitation funding, and there was little interest nor technology to easily and consistently identify unburned islands (Kolden et al., 2012). Only recently, more studies have started focusing on unburned and low burn severity areas because of their potential contribution to ecosystem resilience in the face of climate change and changes in wildfire activity (Meddens et al., 2016).

Meddens et al. (2016) developed a method to delineate unburned islands from spectral data using moderate resolution satellite imagery from the Landsat Thematic Mapper (TM). Satellite sensors such as the TM and its successors have been employed for detecting ecological disturbances and wildfire impacts since 1982, but only since a couple decades, the US fire management community started emphasizing the use of this type of satellite-derived data for identification of wildfire impacts (Eidenshink et al., 2007). With an accuracy of 91.7% and 89.2% in separating burned from unburned locations using two types of classification methods, Meddens et al. (2016) developed a new quantitative analysis to identify the most accurate method for delineation of unburned islands. These results have been used to create an unburned islands database for the Great Basin, which yields a wide array of new applications for the analysis of (sagebrush) ecosystems and their dynamics under the disturbance of fire (Meddens et al., 2016).

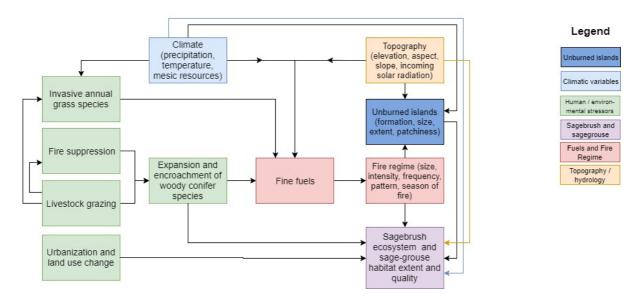


Figure 3: Conceptual diagram of some of the interactions in the sagebrush ecosystems of the Great Basin of North America. Green shows human and environmental stressors and how they affect fine fuels and sage-grouse habitat, as well as how climate and topography affect invasive annual grass species and the formation of unburned islands. In the end all human and environmental stressors negatively affect the fire regime (higher fire intensity, frequency and severity), which in term may affect the formation of unburned islands and the quality and extent of sage-grouse habitat.

1.3 Study Area

The Great Basin is an area characterized by large expanses of conifer forests, salt deserts and sagebrush ecosystems. The dominant shrub and grass species in the study area are Wyoming big sagebrush (A. tridentata subsp. wyomingensis), basin big sagebrush (A. tridentata subsp. tridentata), bluegrass (Poa patensis) and cheatgrass (Bromus tectorum). For the purpose of this research, the study area will encompass the range of sage-grouse in the state of Oregon, United States as determined by the Oregon Department of Fish and Wildlife. Figure 4 shows an overview of the study area. This study area is chosen because it contains a large amount of sagebrush ecosystems with sage-grouse populations, has a rich wildfire history with 231 documented fires larger than 4 km² between 1984-2014, as well as many varied unburned islands of potential interest as observed from the unburned island database by Meddens et al. (2016). In addition, it is one of the few areas with detailed and extensive cheatgrass cover maps. The study area, and accordingly, the range of sage-grouse in Oregon, has a total size of approximately 47257 km². The study area is mostly dominated by sagebrush and grass species, with some patches of conifer forest and agricultural areas. The elevation ranges between 1120-2750 meters, the annual temperature ranges between -6 to 13 degrees Celsius and the annual precipitation averages between 200-700 mm (WorldClim, 2017).

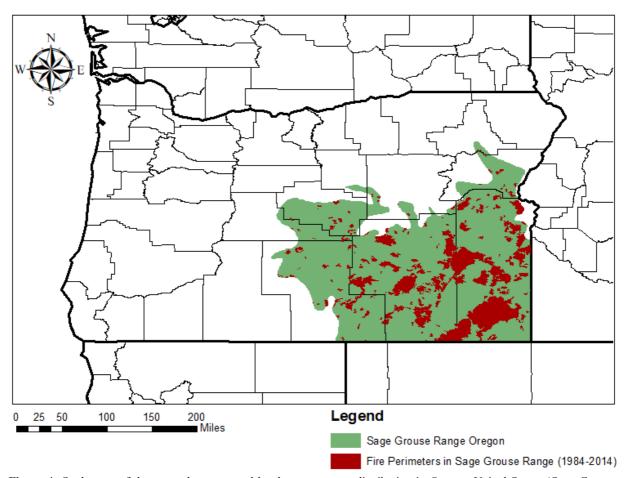


Figure 4: Study area of the research represented by the sage-grouse distribution in Oregon, United States. 'Sage Grouse Distribution Oregon' retrieved from GAP-Analysis (GAP, 2011) and 'Fire Perimeters in eastern Oregon (1984-2014) obtained from MTBS Program (MTBS, 2014)

2. Aims, Objective and Research Questions

The main aim of this research was to assess the effect of wildfire disturbances on the post-fire dynamics of sage-grouse lek populations in south-eastern Oregon. More specifically, this research aimed at understanding the response of sage-grouse lek populations after fire in relation to the spatial distribution of their lek sites and post-fire habitat composition surrounding their respective lek sites. By doing so, this study hoped to find out how sage-grouse lek populations respond to fire if their lek site is situated inside of an unburned island, as compared to if their lek site is located inside of the fire perimeter or near the fire perimeter.

The results of this study could indicate if unburned islands have high ecological importance by functioning as wildfire refugia and allow for the persistence of sage-grouse populations after fire. If this study can successfully identify the specific properties and functioning of unburned islands, these areas may then potentially be located, managed and constructed to ameliorate against the negative effects of fire disturbances on wildlife populations in the future. For these reasons, the research questions for this study are:

- 1. How does the spatial distribution of greater sage-grouse lek populations in or around the fire perimeter affect their response to fire disturbances?
- 2. To what extent does the post-fire habitat composition surrounding lek sites at multiple scales affect their lek population response to fire disturbances and which habitat characteristics and scales are most important in determining this response?

To tackle these questions, this research had the following objectives. First, leks were grouped into four major categories based on spatial location in relation to the fire perimeters: inside of the fire perimeter, inside of unburned islands, < 1500m near the fire and > 1500m near the fire. Second, generalized linear models were created of the pre- and post-fire population trend of every lek site within a specific lek site category. Afterwards, the population trends of each lek site within a lek site category were averaged and compared using mean difference tests to find out if there are dissimilarities between the post-fire population responses of lek site populations from different lek site categories.

Subsequently, the post-fire habitat composition, or the characteristics of vegetation surrounding these lek sites was modelled at multiple spatial scales (0.8km, 6.4km and 18km) known to affect habitat selection pattern of sage-grouse lek populations. Hereafter, the post-fire population trend of each lek site was related to the post-fire habitat characteristics surrounding this respective lek site using univariate and multiple linear regression analyses. These analyses were done to find out if and on which scales, the presence and extent of certain habitat characteristics surrounding lek sites affect the recovery and persistence of their lek populations after fire disturbance. The results of the habitat suitability analyses may indicate the specific properties of unburned islands that are needed to successfully function as refugia for sage-grouse.

3. Materials and Methods

The methodology of this research was split up into two parts. First, the average population trends of each lek site category were retrieved and analysed. Second, the post-fire habitat composition around each lek site was modelled and related to these population trends.

3.1 Post-Fire Population Dynamics

A schematic overview summarizing the methodological steps undertaken to retrieve the preand post-fire population trends of each lek site category can be seen in Figure 5.

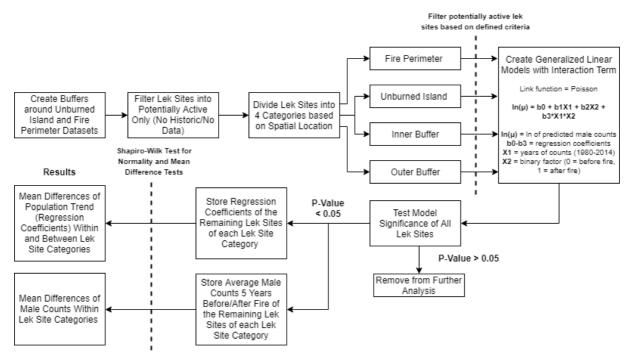


Figure 5: Schematic overview of the methodology to assess the post-fire population dynamics of sage-grouse lek populations. This research part is divided into four steps. First, lek sites are categorized into four categories based on their spatial location. Second, the pre- and post-fire population trend of all lek sites in each lek site category is modelled using a generalized linear model. Third, the pre- and post-fire population trends of all lek sites in each lek site category are averaged. Lastly, mean difference tests are conducted to assess if there is a significant difference between the pre- and post-fire population trend within a lek site category and between lek site categories.

3.1.1 Datasets

To analyse the relationship between the spatial location of sage-grouse lek populations and their post-fire dynamics, the following three datasets were needed: 1) sage-grouse lek population data from the U.S Fish and Wildlife Service, 2) the fire perimeters of 1984-2014 by the Monitoring Trends in Burn Severity (MTBS) program from the U.S Department of Agriculture Forest Service (USDA-FS) and U.S Geological Survey (USGS) and 3) the unburned island dataset from 1984-2014 as created by Meddens et al. (2016). The following sub-paragraphs will explain how and why these datasets were used to assess the post-fire population dynamics of the sage-grouse lek populations in the study area. A summary of the datasets, including spatial resolution, content, time-period and sources are listed in Table 1.

Table 1: Summary of all datasets used to retrieve the population trends of each lek site category. The MTBS and Unburned Island databases are used to understand location of sage-grouse lek populations in relation to the fire perimeter. The sage-grouse population data is used to perform trend analyses on the population data of each lek site, which can then be related to the spatial location of these lek sites.

Name Dataset	Spatial Resolution	Time-Period	Source	Content Description
MTBS Fire Perimeters	Vector layer	1984-2014	https://www.mtbs.gov/	Fire perimeters of all documented wildfires
Unburned Islands Database	30x30 meters	1984-2014	Meddens et al. (2016)	Unburned islands across all documented wildfires
Sage-grouse Population Data	Point Data	1980-2017	Oregon Department of Fish and Wildlife	Range maps, location of leks and population abundance of sage-grouse

Sage-Grouse Lek Population Data

To understand the relationship between post-fire sage-grouse population dynamics and the history of wildfire and presence of unburned islands, spatially extensive and multi-temporal data of lek locations and population abundance over time was needed with which population trend analyses could be performed. This data was obtained from the Oregon Department of Fish and Wildlife, who monitor sage-grouse populations in Oregon. Leks are mating locations for male sage-grouse, which typically occur in the same locations each year. However, lek locations may shift during persistent disturbance or alterations of vegetation cover (Connelly et al., 2011b).

Although methods for gathering these lek counts vary among state-wide agencies, they generally follow the same approach. Typically, leks are visited multiple times per year during breeding season (March-May), between 0.5 hour before sunrise and 1.5 hours after sunrise. Any counts that are done outside of these times are noted as late counts (ODFWS, 2017). At these lek sites, all males strutting a specific lek site are tallied. After the breeding season, when each lek site has been visited multiple times, the peak attendance of male sage-grouse of all the visits is used as the count for that specific year (Connelly et al., 2003; Johnson et al., 2011). The reason why lek counts were chosen for this research is that they are widely used for monitoring of sage-grouse populations. Furthermore, lek counts are presently the only source of data that is suitable for examining trends in population size and their spatial distribution at landscape scale (Connelly et al., 2004).

The datasets that result from lek counting contain yearly counts of male sage-grouse individuals of all documented lek sites in Oregon, as well as up to date range maps. Although in the last decades, relatively few lek sites were counted on a yearly basis, and yearly counts often started at a lek site after it burned, the Oregon Department of Fish and Wildlife aims at increasing the amount of leks that are counted every year to 50% because of the species' high ecological concern and population declines (L. Foster, personal communication, October 6, 2017).

MTBS Fire Perimeters

To monitor the effectiveness of national fire management strategies, the MTBS program was developed to map and assess the burn severity and fire perimeters for all large current and historical fires in the U.S. The fire perimeter is the entire length around the outer edge of a fire. This dataset contains the date, size, extent and severity class of each documented fire between 1984-2014 that is greater than 4 km² (Eidenshink et al., 2007).

The MTBS fire perimeters dataset was used to understand where in relation to the fire, sage-grouse lek populations are located. Using this dataset, the burn year of each specific lek site could be documented, and the lek site could be categorized into one of the four lek categories. Afterwards, the average population trends of these lek site categories could be compared. The fire perimeter dataset was also utilized to distinguish burned from unburned areas during the modelling of the post-fire habitat composition.

Unburned Island Database

The unburned island dataset from Meddens et al. (2016) contains information on the date, size, extent, and vegetation cover of unburned islands within all the wildfire perimeters that were documented by the MTBS between the years 1984-2014. The unburned island dataset has a 30x30 meter resolution, and was used as the base dataset from which the spatial analyses were performed. With the help of this dataset, lek sites could be categorized into the unburned islands category, which is of importance considering one of the main aims of this research is to assess if there are differences in post-fire response between sage-grouse populations inside of unburned islands and those inside of the fire perimeter.

The unburned island dataset was created using moderate resolution Landsat imagery and ancillary data to classify unburned areas within documented wildfire perimeters from the MTBS. Although the MTBS program has similar methods to classify unburned areas, the classification accuracy of the method by Meddens et al. (2016) was significantly higher (90%) than the semi-automated classification from the MTBS. Due to the classification accuracy of 90% for the method used by Meddens et al. (2016), some parts inside of an unburned island are erroneously classified as burned. These areas are therefore filled and made part of the unburned islands using the "Eliminate Polygon Part" function in ArcGIS (Version 10.5.1).

3.1.2 Pre-Processing Lek Population Data

Before the effect of fire and unburned islands on post-fire population dynamics of sage-grouse could be assessed, several data filtering criteria were developed. These criteria evaluated whether a lek site had enough temporal data to be analysed, in addition to dividing leks into four lek site categories based on location inside the fire perimeter or distance from a wildfire perimeter. The filtering process of lek population data can be seen in Figure 6.

Lek sites had sufficient population data when they met the following criteria. First, they had to be potentially active for at least one period between the years 1980-2014. This means that historic lek sites, or lek sites that were only active before 1980, as well as lek sites without any data, were removed. Second, only the lek sites that contained 10 or more counts (>= 30%) during the period from 1980-2014 were included. This was the same approach as a study performed by Johnson et al. (2011), who used the same percentage of required counts. This amount of required counts was chosen because fewer counts would significantly alter the

precision of trend estimates (Johnson et al., 2011). Lastly, the selected lek sites were refined to incorporate only those that were counted at least 2 times during the 5 years before the fire and 2 times in the first 5 years after fire. This was done because it allowed for more accurate differentiation of the direct effects of fire on sage-grouse populations.

The four categories were determined as: fire perimeter (burned area), unburned islands (unburned islands within wildfire perimeter), inner buffer area (area between 0-1500 meters around wildfire perimeter) and outer buffer area (area between 1500-6400 meters around wildfire perimeter). The maximum radius of 6.4 kilometres was decided because more than 80% of female sage-grouse distribute their nests in an area of 6.4 km around lek sites (Hagen, 2011a). Additionally, Walker et al. (2007) recommended it as a suitable range to measure landscape scale processes such as loss of nesting habitat from disturbances. For these reasons, it is assumed in this research that if lek sites are located farther from a fire than the 6.4km range, the effects of fire on sage-grouse populations are neglectable.

In the study area, the Oregon Department of Fish and Wildlife documented 1179 lek sites. From these lek sites, it was found that only 766 lek sites contain enough male counts data for a spatio-temporal analysis on population dynamics between the years 1980-2014. The other lek sites did not meet the criteria because they were either denoted as historic, indicating that they have been unoccupied since before 1980, or that they did not contain any population counts at all. After performing the selection process for the lek site data, a total of 73 suitable lek sites remained for analysis. Of these 73 lek sites, 12 were situated inside of the fire perimeter, 7 inside of unburned islands, 15 inside of the inner buffer and 39 inside of the outer buffer (see Figure 6).

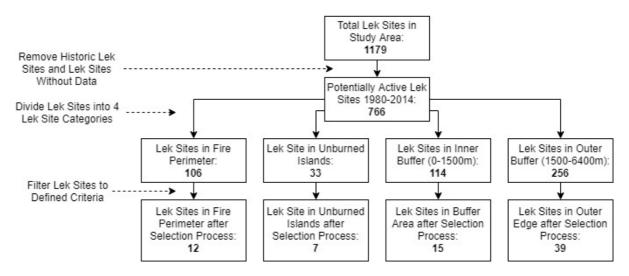


Figure 6: Schematic overview of the lek site data and its distribution over the study area of south-eastern Oregon after selecting using defined criteria. Of the 1179 lek sites in south-eastern Oregon, only 766 were not historic and contained actual data counts. After categorizing based on spatial location, leks were divided as follows: 106 in fire perimeter, 33 in unburned islands, 114 in inner buffer and 256 in outer buffer. After filtering for sufficient data (at least 2 counts in the 5 years before and after the fire, and at least 10 counts over the period 1980-2014), each lek site category remained with the following amount of usable lek sites for analysis: fire perimeter (12), unburned island (7), inner buffer (15), outer buffer (39).

3.1.3 Statistical Analyses

Generalized Linear Models

To analyse the effect of wildfire on sage-grouse populations and the influence of spatial location of lek sites on their lek population persistence, generalized linear models (GLM) were created for each lek site within a lek site category. By doing so, pre- and post-fire population trend values could be retrieved for each lek site. These trends could then be averaged and compared for each lek site category to answer the question as to if there are differences in lek population response to fire due to the spatial location of their lek sites. For this research, GLM's were chosen over other options as count data is often positively skewed with many low-count observations. Thus, standard linear regression would in this case lead to biased results (Coxe et al., 2009). Using a link, GLM's have the option to take on a different probability distribution than Gaussian, which is needed in cases where data is not normally distributed. In this research, the Poisson link function was used, as the Poisson distribution is a discrete distribution of non-negative integers with a highly positive skew at low means under 10. This is highly similar to count data. As a result, the dependent variable was specified as a Poisson variable, whose means are multiplicatively related to the independent variables as a natural logarithm as compared to additively in simple linear regression models (Nelder and Baker, 1972). Additionally, an interaction term was added for fire history. Interaction terms are used if it is suspected that the independent variables work jointly (i.e. interact) instead of additively (Cortina, 1993). By adding this interaction variable, the GLM's that were created for each lek site contain a separate pre- and post-fire population trend for the lek site, which could then be used to compare the average population trend of each lek site category before and after the fire, which is one of the main questions of this study. In the case of this research, the interaction term was represented by a factor, in which 0 meant before fire and 1 meant after fire. Male sage-grouse were predicted over time using the years in which male sage-grouse were count, together with the binary interaction term which indicated if a year is before or after a fire. Consequently, the formula for the GLM's was as follows:

$$ln(\hat{\mu}) = b0 + b1X1 + b2X2 + b3*X1*X2$$

In which:

 $ln(\hat{\mu})$ = natural logarithm of male sage-grouse counts

b0 = intercept

b1-b3 = regression coefficients of predictor variables

X1 = years in which sage grouse were count (1980-2014)

X2 = factor (0 = before fire, 1 = after fire)

b3*X1*X2 = interaction term

Mean Difference Tests of Population Trends

Using the results of the GLM's, which contain the pre- and post-fire population trends of each lek site in their respective lek site category, mean differences tests could be conducted to assess if the average population trends within and between lek site categories differs before and after fire. With this information, the research question could be answered that asks if lek populations respond differently to fire depending on the spatial location of their respective lek sites, as well assessing if unburned island lek populations are not negatively affected by fire.

Before these mean difference tests could be conducted, the pre- and post-fire population trend results of each GLM were first assessed on their significance. If a model trend of a lek site had no statistical significance (p-value > 0.05), indicating that the population was extirpated from that specific lek site even before the fire (and consequently, no significant trend exists), it was removed from further analysis. Hereafter, the pre- and post-fire population trends of each lek site category are stored and averaged. In the end, every lek site category has one exponential pre- and post-fire population trend, which is an average of the population trends of all lek sites in that specific lek site category. With these values, the mean difference tests can be carried out.

Before the mean difference tests were carried out, a Shapiro-Wilk test was performed on the average pre- and post-fire population trends of each lek site category. This was done to test if the set of data was distributed according to the normal probability distribution using its variance (Shapiro and Wilk, 1965). If the data was normally distributed, a two-sided t-test was performed. If the data was not normally distributed, a non-paired Wilcoxon signed-rank test was performed, which is the nonparametric test for mean differences. Assessing for normal distribution is important, because performing a t-test on a sample of population trends which is not normally distributed can give un-meaningful and incorrect results.

The results of the mean difference tests could be used to analyse the response of sage-grouse lek populations to fire in relation to their spatial location. First, the pre- and post-fire population trends were compared within each lek site category to see if the population within a lek site category changes significantly after fire or not. Second, differences between the pre- and post-fire population trends of separate lek site categories were examined. By doing so, it could be evaluated if the average population response to fire is significantly different between lek site categories. This information could then be used to understand if unburned island lek site populations react differently to fire than those inside of the fire perimeter. In addition to performing mean difference tests for the population trends of each lek site category, these tests were repeated for the male sage-grouse counts. For each lek site within a lek site category, the male counts of the 5 years before were averaged, after which difference tests were repeated for the male counts of the 5 years after the fire. By determining if there are differences in male sage-grouse abundance in the first 5 years after fire as compared to the years before fire, a more direct and short-term effect of fire on sage-grouse populations could potentially be distinguished for each lek site category.

In short, the results from these statistical analyses indicate for each lek site category if there is a significant difference in the population trend and absolute number of male counts after fire as compared to before the fire. If there are no significant differences in the population trend and male sage-grouse counts before and after fire, for example within the unburned island lek site category, this could indicate that unburned islands may function as wildfire refugia and allow for the persistence of these lek populations. Additionally, if there is a significant difference between the post-fire population trend of fire perimeter and unburned island lek sites, this could indicate that unburned island lek populations generally react differently to fire as compared to fire perimeter lek populations. Such information can be used to understand how the spatial location of lek populations influences their response to fire, which is one of the main aims of this research.

3.2 Post-Fire Habitat Composition and Suitability

To assess the effect of post-fire habitat composition on the dynamics of sage-grouse populations after fire, two types of analyses were conducted with the following objectives. First, deductive habitat suitability models were created of the post-fire landscape using Geographic Information System (GIS) technology. These habitat suitability models show where in the burned landscape surrounding a lek site, a specific habitat characteristic is suitable or unsuitable. Second, the results from these habitat models were converted to a metric that represents percentage of suitable habitat around a lek site. These new values could then be used to perform linear regression analyses between the population trends and the post-fire habitat suitability, as well as conducting statistical tests on the differences between mean habitat characteristics of unburned island and fire perimeter lek sites. The results of these analyses could then answer the research question as to if the post-fire habitat composition surrounding lek sites is a major factor in determining the persistence of their respective lek populations and which habitat characteristics and scales are most important.

Figure 7 shows a schematic overview which summarizes the methodological steps undertaken to model the post-fire habitat composition surrounding lek sites and their relationship with the post-fire population trend of these lek sites.

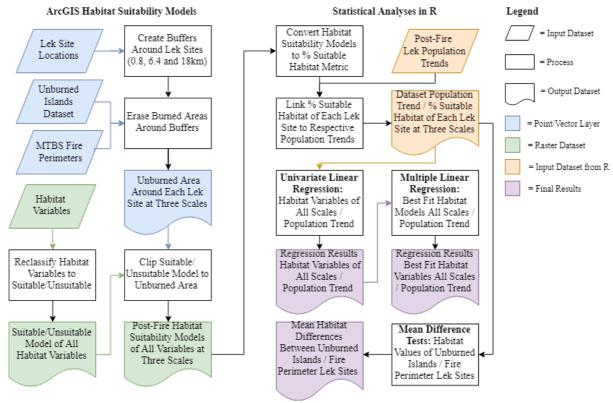


Figure 7: Schematic overview of the methodology to analyse the relationship between post-fire habitat composition surrounding lek sites and their population response after fire. First, the analysed lek sites, unburned island dataset and fire perimeter dataset are used to model the unburned area surrounding a lek site at each of the three spatial scales (0.8km, 6.4km and 18km). Afterwards, the habitat suitability of this unburned area is modelled using the known ecological requirements of sage-grouse for vegetation characteristics. The results of these models are then converted to the Habitat Suitability Percentage (HSP), a metric that represents on each spatial scale, the percentage of suitable unburned area surrounding a lek site divided by the total area surrounding that lek site at each spatial scale. Afterwards, univariate and multiple regression analyses are performed to assess the relationship between these habitat variables and the post-fire population trend. Lastly, mean difference tests are performed to evaluate the habitat characteristics of unburned island lek sites as compared to fire perimeter lek sites, to see if unburned island have higher vegetation suitability which may explain their dissimilar population response after fire.

3.2.1 Datasets

For this study, deductive habitat suitability models were created for the following habitat variables: vegetation type, vegetation cover, vegetation height, cheatgrass cover and distance to mesic resources. Specifically these habitat variables were chosen because it is well-known how their characteristics affect sage-grouse habitat selection and when these characteristics are suitable or not. Unburned area was also included as a variable for both the statistical analyses and as a physical boundary for the habitat suitability models, as it is one of the most important factors in the determination of overall post-fire habitat composition.

As a result, to be able to model the post-fire habitat composition surrounding the previously analysed lek sites and relate their suitability to the post-fire population trend of these lek sites, the same datasets that were used during the analysis of post-fire population dynamics were used during the habitat suitability analysis. In addition, several vegetation and hydrography datasets from the LANDFIRE program and USGS were used which represent the characteristics of vegetation in the study area. In all cases, the habitat datasets that were used to create the habitat suitability models were time-specific and matched the period when the lek site first burned. For example, if a lek site burned in 2012, the most recent vegetation maps of 2010 and the cheatgrass map of 2012 were used. A summary of these datasets, including spatial resolution, content, time-period and sources are listed in Table 3.

Table 2: Summary of all used datasets during the deductive habitat suitability analysis surrounding lek sites. The same MTBS fire perimeters, unburned islands and sage-grouse lek population data are used as the assessment of post-fire population dynamics, this time to delineate burned and unburned area surrounding each lek site. The cheatgrass map, vegetation maps and hydrography maps of the sage-grouse range in south-eastern Oregon are utilized to model their

suitability for sage-grouse in the unburned area surrounding each lek site.

Name Dataset	Spatial Resolution	Time- Period	Source	Content Description
MTBS Fire Perimeters	Vector Layer	1984- 2014	https://www.mtbs.gov/	Fire perimeters of all documented wildfires
Unburned Islands Database	30x30 meters	1984- 2014	Meddens et al. (2016)	Unburned islands across all documented wildfires
Sage-Grouse Lek Site Population Data	Point Data	1980- 2017	Oregon Department of Fish and Wildlife	Range maps, location of leks and lek population size
Cheatgrass Map	250x250 meters	2000- 2015	Boyte et al. (2016)	Cheatgrass cover in the Great Basin
Vegetation Characteristics	30x30 meters	2001- 2014	https://landfire.cr.usgs.gov/	Vegetation types, cover and height
Hydrography	Vector Layer	2011 (released)	http://spatialdata.oregonexplorer.info/geoportal/	Hydrological features (streams/water bodies)

3.2.2 Determination of Habitat Suitability

The suitability thresholds used for each habitat variable in the habitat suitability will be explained in the upcoming paragraphs.

Scale

Before the habitat suitability models could be created, the appropriate scales (buffer) around each lek site for the analyses were determined at 0.8km (201ha), 6.4km (12,867ha) and 18km (101,787 ha). These three scales were chosen for the habitat suitability analyses because they each represent processes that impact sage-grouse habitat selection in different ways. The 0.8km scale was selected as the smallest scale because it represents processes that impact breeding and nesting birds near leks (Walker et al., 2007). Furthermore, during the breeding and nesting season, sage-grouse cocks hardly move farther away than 1km from leks (Wallestad and Schladweiler, 1974). The 6.4km scale was decided because it reflects processes that occur on a larger spatial scale, such as loss of nesting habitat (Walker et al., 2007), and because females generally distribute their nests within a radius approximately 6.4km from a lek site (Hagen, 2011). The 18km radius scale was chosen as it reflects a landscape scale, and is also the recommended distance around lek sites used for management of migratory sage-grouse populations (Johnson et al., 2011).

Unburned Area

To represent the remaining unburned area around each lek site after fire, which was used to model suitability inside of this unburned area, a raster dataset was created for each scale that contains the buffer range (scale) around each lek site minus the burned landscape. To create this feature, the fire perimeters dataset (1984-2014) from MTBS was used in ArcGIS together with the unburned island database (1984-2014) from Meddens et al. (2016). First, all holes in the unburned island dataset that were created by incorrect classification were filled, after which they are erased from the fire perimeters dataset. Consequently, the newly created fire perimeter dataset contains all fire perimeters excluding the unburned islands within these fire perimeters.

To delineate unburned area around each individual lek site, the newly created fire perimeters (without unburned islands) of the burn year and 17 years prior to the burn year were selected and erased from the buffer around this specific lek site. The remaining raster contained on all three scales the area around the lek site, including unburned islands, that was not burned in the 17 years prior to the fire that burned in or near that specific lek site. The time range of 17 years was chosen because the earliest available vegetation map is from 2001, which is 17 years after the earliest documented fire in the MTBS fire perimeters dataset in 1984. For this reason, several lek sites that were analysed in the post-fire population dynamics analysis but burned in a year before 2001 were excluded from the post-fire habitat composition and suitability analysis, as no detailed and time-specific vegetation and cheatgrass cover maps were available for this time period. An example of the unburned area dataset, which was used to model the habitat suitability of the unburned area, can be seen on a 6.4km scale in Figure 8.

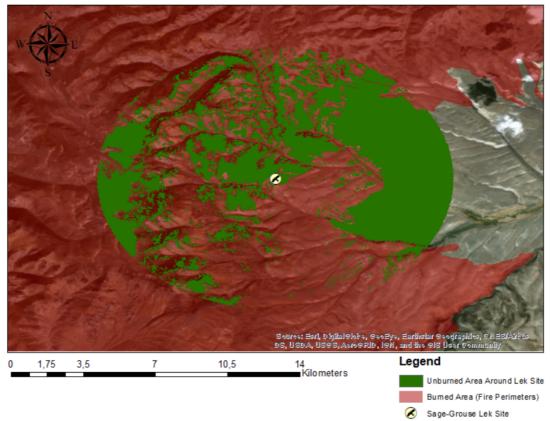


Figure 8: Unburned area around the Dry Creek #2 lek site inside of the Holloway Fire of 2012 (6.4km scale). Area in green is, on a 6.4km scale, the unburned area in the 17 years before the fire that burned around the specific lek site (including unburned islands). Red shows the burned area surrounding the Dry Creek #2 lek site.

Vegetation Types

To assess which vegetation types in the buffer area around a specific lek site were labelled as suitable or unsuitable in the deductive habitat suitability model, the multi-temporal vegetation type maps from LANDFIRE were consulted. If a vegetation type in the LANDFIRE maps corresponded with a suitable vegetation type for sage-grouse according to literature, it was given a suitable value. Similarly, habitats without known use by sage-grouse, such as barren and developed areas (Holloran, 2005; Carpenter et al., 2010), as well as alpine and forest habitats (Schroeder et al., 2004) were logically categorized as unsuitable. Table 3 shows suitable vegetation types for sage-grouse that also occur in the LANDFIRE vegetation type maps from 2001-2014.

Table 3: Suitable vegetation types for sage-grouse in sagebrush ecosystems. Each row explains a specific vegetation type with example species, as well as their suitable characteristics for sage-grouse and the literature sources that argue why this specific vegetation type is suitable for sage-grouse.

Vegetation Type	Suitable Characteristics	Literature Source
Big Sagebrush (Artemisia tridentata, subsp: vaseyana, wyomingensis)	Source of food and cover	Welch et al., 1991; Barnett and Crawford (1994); Schroeder et al. (2004); Arndt and Black (2011);
Low Sagebrush (Artemisia arbuscula)	Source of food and cover	Gregg et al. (1994); Drut et al. (1994a); Drut et al. (1994b); Gregg et al. (2008)

Shrubs, i.e: Saltbush (Atriplex spp.) Greasewood (Sarcobatus vermiculatus) Green Rabbitbrush (Chrysothamnus viscidiflorus) Bitterbrush (Purshia tridentata)	Secondary food source and cover	Wallestad (1971); Gregg et al. (1994); Schroeder et al. (2004); Arndt and Black (2011); Hagen (2011)
Forbs, i.e: Desert-parsley (Lomatium spp.) Hawksbeard (Crepis spp.) Phlox (Phlox spp.) Clover (Trifolium spp.) Dandelion (Agoseris spp.)	Important source of food	Klebenow and Gray (1968); Wallestad and Eng (1975); Barnett and Crawford (1994)
Grasses, i.e: Bluebunch Wheatgrass (Pseudoroegneria spicata) Sandberg Bluegrass (Poa sandbergii) Great Basin Wildrye (Elymus cinereus)	Important nesting and breeding cover	Gregg et al. (1994); DeLong et al. (1995); Schroeder et al. (2004); Arndt and Black (2011)

Vegetation Cover

To assess which minimum percentage of vegetation cover is suitable for sage-grouse, habitat suitability models of vegetation cover were created using five different vegetation cover thresholds. Afterwards, a sensitivity analysis was performed to examine which vegetation cover threshold results in the best linear regression model output. The model with the best fit vegetation cover percentage would then be used as the suitability threshold. This was done because although it is known that there is a strong relationship between vegetation cover and habitat use by sage-grouse, the minimum required vegetation cover that is needed for long-term sage-grouse population persistence and survival is debated. An overview of the five different vegetation cover thresholds used for the sensitivity analysis, as well as their rationale, can be seen in Table 4.

Table 4: Minimum required vegetation cover for long-term persistence of sage-grouse in sagebrush ecosystems. Every row shows the percentage of vegetation cover, together with a rationale and literature sources that argue why this minimum

percentage of vegetation cover is needed for sage-grouse.

Vegetation Cover Threshold (%)	Rationale	Literature Source
20%	 Minimum required cover for successful nesting is 15% Long-term persistence requires minimum of 25% cover 	Wallestad and Pyrah (1974); Aldridge et al. (2008); Wisdom et al. (2011)
30%	Low probability of persistence with <30% sagebrush cover	Walker et al. (2007)
40%	 90% Of active leks contain at least 40% sagebrush cover >= 40% Shrub canopy cover improves reproductive 	Knick et al. (2013); Lockyer et al. (2015)

	success	
50%	 Highest probability of persistence with > 50% sagebrush cover Mean sagebrush cover of 51% and 59% over 2 years 	Wisdom et al. (2011); Sveum et al. (1998)
60%	More than 65% sagebrush cover required at landscape scale for long-term persistence	Aldridge et al. (2008)

Vegetation Height

In this research, the suitability threshold for vegetation height was set to 0.5 meters height. This was done for two reasons. First, the vegetation height maps from LANDFIRE break down vegetation height in classes of 0.5 meters. Second, literature suggests that sage-grouse preferably use relatively high stands of vegetation of about 0.5 meters and higher as it strongly influences nesting success and survival during winter. Table 5 shows an overview of various studies that document the average vegetation heights of habitat used by sage-grouse throughout different seasons, on which the suitability threshold for vegetation height in this research was based.

Table 5: Vegetation height of habitat used by sage-grouse during various seasons. Each row shows the mean vegetation height used by sage-grouse during that specific season, together with the literature source of the paper that assessed the height of vegetation used by sage-grouse. Based on these values, the vegetation height suitability threshold is set to 0.5 meters.

Vegetation Height (centimetres)	Season of Habitat Use	Literature Source
40	Spring (Nesting)	Wallestad and Pyrah (1974)
40-80	Spring (Nesting)	Gregg et al. (1994)
46	Winter	Robertson (1991)
69	Spring/Summer (Breeding, Nesting and Brood-Rearing)	Apa (1998)
71	Spring/Summer	Wakkinen (1990)
80	Spring/Summer (Nesting and Brooding)	Keister and Willis (1986)

Cheatgrass Cover

Similar to vegetation cover, there is inconsistency in the maximum cover of invasive grasses that still allow for the long-term persistence of sage-grouse populations. As a result, the habitat suitability models for cheatgrass cover were also created multiple times with three different cheatgrass cover percentages as suitability thresholds. Afterwards, a sensitivity analysis was conducted for each model to find the cheatgrass cover percentage that offers the best model outputs, and therefore was used as the suitability threshold for cheatgrass cover in the habitat suitability models for cheatgrass cover. An overview of the three suitability thresholds and their rationale can be seen in Table 6.

Table 6: Maximum cheatgrass cover that allows for persistence of sage-grouse populations according to previous research,

including rationale and literature source.

Cheatgrass Cover Threshold (%)	Rationale	Literature Source
2%	Active leks have on average a maximum of 2.2% invasive grass species	Knick et al. (2013)
7%	Average cheatgrass cover on selected nesting sites by sage-grouse is 7.1% as compared to 13% at random areas	Lockyer (2012)
8%	On a landscape scale (5km and 18km), few active leks had > 8% cheatgrass cover	Johnson et al. (2011)

Distance to Mesic Resources

To assess suitable distance to mesic resources of sage-grouse lek sites, a dataset from the USGS was used that contains hydrographical features in the study area, such as water bodies and streams. Donnelly et al. (2016) found that sage-grouse population abundance is strongly related to the distribution of mesic resources, where the highest density breeding populations were located closer to productive mesic sites. The highest density active lek sites were found where mesic resources were located within 3.3 kilometres of a lek site. However, moderate population abundance was found if lek sites were located between 3.3-4 kilometres from a lek site. For this reason, a sensitivity analysis was conducted using both input distances as a suitability threshold, where the suitability threshold of the best fit model will be used as the threshold for further analysis.

3.2.3 Statistical Analyses

Habitat Suitability Percentage

After the deductive habitat suitability models were created for every lek site on all three scales for the five habitat variables, their resulting values were further processed in the computer programming environment R (Version 1.0.153). Each habitat suitability model that was created in ArcGIS contains, on every scale, the amount of unburned cells (30x30m) surrounding a lek site that are suitable or unsuitable for the specific habitat variable. For linear regression analyses to be done with this data, these values were converted to a metric that more logically represents the percentage of suitable habitat in the area, while also being adjusted for the amount of unburned area that is left around a lek site. Ultimately, the results of these analyses could then show if there is a relationship between the quantity and quality of a certain habitat characteristic surrounding a lek site and its post-fire sage-grouse population trend. This is one of the main objectives of this research. The formula for this conversion is as follows:

$$HSP = SU/TU * (TU/TA)$$

Where:

HSP = Habitat Suitability Percentage

SU = Suitable Unburned Area

TU = Total Unburned Area

TA = Total Area around a Lek Site

This conversion indicates that besides the quality of the remaining habitat, the amount of unburned area was important in the determination of the habitat suitability percentage (HSP). The lower the proportion of unburned area is, the lower the habitat suitability percentage becomes, regardless of the unburned area habitat quality. This assumption has been made for this research because in general, it makes more sense from an ecological perspective for larger patches of vegetated unburned islands to be of higher ecological value than smaller unburned islands (Longland and Bateman, 2002).

After all habitat suitability models were converted to the HSP values, they were stored separately in a dataset for each individual spatial scale. Only the HSP values for the cheatgrass variable were stored differently. These values were stored using the formula: 1-HSP. By doing so, the relationship between the population trend and cheatgrass cover likely becomes negative, such that an increase in the proportion of area with unsuitable cheatgrass cover reduces the post-fire population trend, which is expected based on knowledge from literature.

In the end, every spatial scale has an own dataset which contains the HSP values for all habitat variables for each analysed lek site. With the help of these datasets, multi-scale univariate linear regression analyses were performed using the HSP values of all analysed lek sites. This was done to assess the relationship between the habitat characteristics surrounding these lek sites and their post-fire population trend. An overview the output datasets for each spatial scale can be seen in Table A2, A3 and A4 in the appendix of this paper.

Univariate Linear Regression

Using the datasets with the HSP values of each lek site, univariate linear regression analyses were performed between the post-fire population trend and every habitat variable of all lek sites on all three scales. By doing so, it could be found out if and on which scale there is a relationship between the post-fire population trend of lek populations and their surrounding post-fire habitat characteristics.

The univariate regression models were also tested using a quadratic relationship. If the resulting model of the quadratic relationship fit the data better, it was used instead of the linear model. The output results of the univariate regression analyses are models of all habitat variables on all three scales. These models show if, how and at which scale, the analysed habitat variables surrounding lek sites are related to their post-fire population trend. This could then show if populations from certain lek site categories, such as unburned islands, respond differently to fire due to the quality and quantity of the remnant post-fire habitat surrounding this lek site.

Afterwards, the univariate models at different scales were competed against each other to identify the most relevant scale for each habitat variable. The scale of the model that best fit the relationship between that specific habitat variable and the population trend was stored in a separate dataset. In the end, this lead to one new dataset that contained the best fitting models of all habitat variables from all scales. These were then be used for the multiple linear regression analysis, which was done to assess which habitat variables are most important in determining the population trend of lek site populations.

Multiple Linear Regression

With the help of the new best fit dataset from the univariate linear regression analyses, a multiple regression was performed between the best fit habitat variables from every scale and the population trends of all lek sites. By doing so, it could be determined which of the evaluated habitat variables surrounding all lek sites is most important in determining the post-fire population trend of sage-grouse lek populations. In the multiple regression analysis, unburned area was excluded as a predictor variable as it is already included indirectly in the HSP from the habitat variables. Using all habitat variables, the multiple regression formula is as follows:

$$Y = \beta 0 + \beta 1X1 + \beta 2X2 + \beta 3X3 + \beta 4X4 + \beta 5X5 + \varepsilon$$

In which:

Y = predicted post-fire sage-grouse population trend (exponential)

 $\beta 0 = intercept$

 $\beta 1-\beta 5$ = regression coefficients of predictor variables

X1-X5 = HSP values of all best fit habitat variables (vegetation types, vegetation cover, vegetation height, cheatgrass cover and distance to mesic resources)

 $\varepsilon = \text{error term}$

The result of the multiple regression analysis is a model that describes the relationship between the post-fire population trend of sage-grouse lek populations and their surrounding post-fire habitat vegetation composition, rather than solely one habitat variable at a time. The predictor variables were tested on both multicollinearity using the Variance Inflation Factor (VIF) and on variable importance using stepwise regression through the Akaike Information Criterion (AIC). If a predictor habitat variable was irrelevant according to the stepwise regression analysis, meaning that its absence increased model parsimony, it was removed from the multiple regression model. In the end, this lead to a new model that included only those habitat variables that best relate to the post-fire population trend of the lek populations.

Mean Habitat Differences

After the regression analyses were conducted, mean differences tests were performed separately on all scales between the average HSP values of lek sites inside of the fire perimeter and those inside of unburned islands. This was done to find out if there are significant differences in the habitat characteristics between lek sites located inside of an unburned island and those inside of fire perimeters. If both the average post-fire population trend and average habitat characteristics of unburned island lek sites were significantly higher than those of fire perimeter lek sites, this would indicate that the post-fire habitat composition surrounding lek sites is important in determining the post-fire population response of lek populations. This is one of the main hypotheses of this research. On the other hand, if there were no significant differences between the habitat characteristics of unburned island and fire perimeter lek sites, but there is between the population trends, this could indicate that unburned islands may have unique characteristics unrelated to habitat composition that allow for persistence of sage-grouse lek populations, which is an interesting finding that is in contrast to the main hypotheses of this research.

Secondary Analyses

To assess whether some lek sites with significantly higher or lower exponential post-fire population trends than other lek sites disproportionately influenced model selection and interpretation, all data was re-analysed with reduced datasets of lek sites. Initially, the lek sites with outliers in post-fire population trend were removed. Afterwards, the univariate regression models were repeated without the outlier lek sites. This was done to see if analysis with reduced datasets yielded in meaningful changes in model fit, model selection and interpretation of results. The results of these analyses will be dealt with in a separate paragraph in the results.

4. Results

4.1 Post-Fire Population Dynamics

4.1.1 Long-Term Population Trend

Based on the performed GLM's with the population trends, it was found out that of all 73 lek sites, only 34 lek sites have a significant trend before or after the fire. Of the remaining lek sites, 7 are located in fire perimeters, 5 in unburned islands, 6 in the inner buffer area and 16 in the outer buffer area. The resulting population trends of each lek site can be seen in Table A1 in the appendix. Additionally, several population trends of lek sites that are indicative for their respective lek site category can be seen in Figure 9.

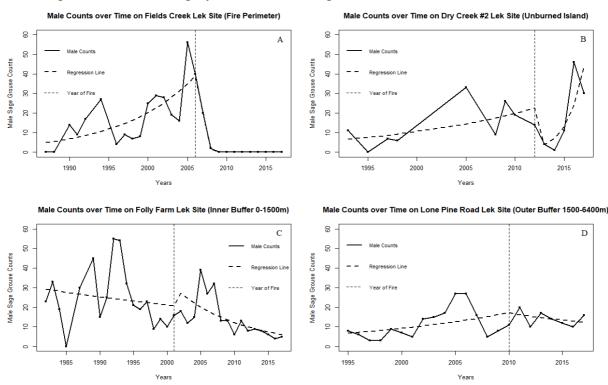


Figure 9: Male sage-grouse counts over time on an indicative lek site inside of (A) the fire perimeter, (B) an unburned island, (C) the inner buffer and (D) the outer buffer lek site category. The dotted vertical line shows the fire year and the horizontal dotted line shows the pre- and post-fire regression line.

The results of the mean difference tests using the average population trends of each lek site category show several interesting findings that can answer the research question as to how the spatial distribution of lek populations affect their dynamics to fire. To begin, it can be seen from Figure 10 that sage-grouse lek populations situated inside of the fire perimeter are significantly negatively affected by fire (p-value = 0.0038, t = 4.2905, df = 6.8443). Whereas the average exponential population trend of fire perimeter lek populations was 1.03 before fire (increase of 3% per year), the average post-fire population trend is 0.59, indicating a population decline of 41% per year after fire. Second, in contrast to fire perimeter lek populations, Figure 10 shows that unburned island lek populations are not significantly affected by fire. Where their average exponential population trend before the fire is 1.06, their post-fire population is not significantly different (p-value = 0.69, W = 15), and in absolute terms even shows an average population increase after fire with an exponential population trend of 1.24.

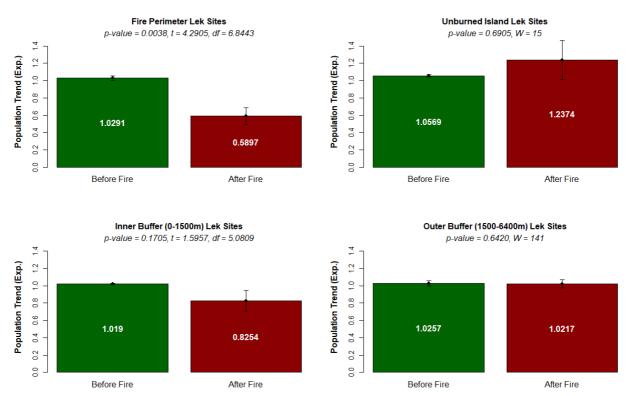


Figure 10: Average exponential pre- and post-fire sage-grouse lek population trend values of each lek site category (fire perimeter, unburned island, inner buffer and outer buffer). Sample sizes for each average population trend were 7 for fire perimeter, 5 for unburned islands, 6 for inner buffer and 16 for outer buffer. The bar graphs indicate that fire perimeter lek populations are significantly negatively affected by fire, whereas the other three lek site categories are not significantly negatively affected by fire disturbances. Test statistics of mean difference tests within each lek site category are shown above each bar graph. Error bars show Standard Error (SE).

Thirdly, although not a significant effect, the results show that on average, sage-grouse lek populations of the inner buffer lek sites (0-1500 meters away from the fire) decline slightly after fire, with an average exponential post-fire population trend of 0.82. This is because the "Egli Rim North", "Larry's" and "Thirsty Hog" lek sites inside of the inner buffer all have exponential post-fire population trends of 0.72, 0.53 and 0.54 respectively (see Appendix A1). This is a population decline of similar magnitude to the average post-fire population trend of lek populations within the fire perimeter. This result is unexpected, considering it is hypothesized that lek populations with lek sites outside of the fire perimeter are not negatively affected by fire. Lastly, Figure 10 shows that lek populations within the outer buffer, at least 1500 meters away from burned area, are not affected by fire, as their population trends remains nearly the same. Additionally, after testing for mean differences between the pre- and post-fire population trend of fire perimeter and unburned island lek sites, it was found that the population trends were not different before fire at the 0.95 confidence level (t = -0.896, df = 9.453 and p-value = 0.392). However, after fire, there is now a difference between the postfire population trends of unburned island and fire perimeter lek sites (t = -2.631, df = 5.554and p-value = 0.042), where the average exponential post-fire population trend of unburned island lek sites is significantly higher with 1.24 versus 0.59 for fire perimeter lek populations.

In short, these results show that sage-grouse lek populations indeed respond differently to fire depending on the spatial location of their lek sites, which therefore answers research question one, asking if lek population respond differently to fire based on the location of their lek site in relation to the fire. The results of these analyses demonstrate that

fire perimeter lek populations are significantly negatively affected by fire, whereas lek populations inside of unburned islands persist and are not negatively affected. This supports the first hypothesis of this research, indicating that sage-grouse lek populations are negatively affected by fire if their respective lek sites burns, whereas unburned islands may allow for the persistence of their sage-grouse lek populations by acting as wildfire refugia after fire.

4.1.2 Short-Term Effects on Male Counts

In addition to analysing differences in the pre- and post-fire population trend between lek site categories, the average male counts in the 5 years before and after the fire were also assessed to address more direct effects of fire on the average male counts in the first years after fire. From these results, which can be seen in Figure 11, similar findings can be observed to the population trend values. Here, opposite to fire perimeter lek sites, the average male counts in unburned islands do not decrease significantly in the first 5 years after fire (p-value = 0.4026, t = -0.91532, df = 4.9273). On the other hand, it can be seen that in the first 5 years after fire, the population inside of unburned islands does decline on average by approximately 45% from 42 to 23 male counts, even though the average post-fire population trend of unburned island lek sites is increasing on the long-term. This indicates that though unburned islands allow for the long-term persistence of sage-grouse lek populations, lek populations inside of unburned islands may still be affected negatively in the first years after fire. This is in slight contrast with the first hypothesis of this research, which suggests that unburned island lek populations are not negatively affected at all by fire disturbances. However, these results still support the hypothesis that sage-grouse lek populations are significantly negatively affected if their lek site is situated inside of the fire perimeter.

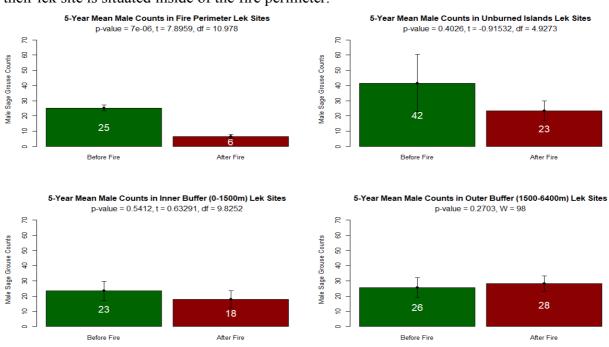


Figure 11: Average male counts of each lek site category over the 5 years before and after fire, together with the p-value of the mean difference test between this data. Sample size for every lek site category is: 7 for fire perimeter, 5 for unburned islands, 6 for inner buffer and 16 for outer buffer. These results show that in the 5 years after fire, the population in fire perimeter lek sites decreases significantly after fire, whereas unburned island lek populations do not decline significantly, even though the population does decline by approximately 45% in the first 5 years after fire. In the first 5 years after fire, the buffer lek populations are not affected negatively. Test statistics of mean difference tests within each lek site category are shown above each bar graph. Error bars show Standard Error (SE).

4.2 Post-Fire Habitat Composition and Suitability

An overview of the habitat suitability percentage values of all lek sites on each spatial scale can be seen in Table A2, A3 and A4 in the Appendix at the end of this paper. Although 34 lek sites were analysed during the post-fire population dynamics part of this research, 5 of these lek sites burned before 2001. Consequently, habitat composition around these lek sites could not be modelled as no vegetation datasets are present for the period before 2001. The dataset of lek sites for the habitat composition analysis consisted of 29 lek sites, with 7 lek sites inside the fire perimeter, 5 in unburned islands, 6 in the inner buffer and 10 in outer buffer.

4.2.1 Univariate Linear Regression

To assess which suitability threshold was decided upon for the habitat variables of vegetation cover, cheatgrass cover and distance to mesic resources, several sensitivity analyses were performed to assess which threshold gave the best model predictions. From these sensitivity analyses, it was found that a suitability threshold for vegetation cover of \geq 20% gave the best model fit. Additionally, for cheatgrass cover, a suitability threshold of =< 8% cheatgrass cover resulted gave the best model results whereas for distance to mesic resources, a suitability threshold distance of <3.3km predicted the population trend best.

The univariate regression analyses were performed to assess which habitat characteristics and spatial scales best explain the post-fire population trend of lek populations. The model results of the univariate linear regression analyses of each habitat variable on each scale can be seen in Table 7. In general, these results show that the models with the habitat variables on the 0.8km scale and 6.4km scale best explain the post-fire population trend, whereas models at the 18km scale perform well only in some cases, such as with vegetation height and cheatgrass cover. This information helps to partially answer research question two, which asks at which spatial scale habitat composition is most important in determining the post-fire population trend of sage-grouse lek populations.

From the model results overview in Table 7, it can be observed that the models of both vegetation height and cheatgrass cover perform best on all three spatial scales. On a 0.8km and 6.4km scale, vegetation height has a strong positive relationship with the post-fire sage-grouse lek population trend. It performs well as a standalone habitat predictor, with coefficients of determination (r-squared) of 0.41 (p-value = 0.0001) and 0.44 (p-value = 8e-05) respectively. However, it must be noted this model parameter is relatively poorly estimated as the standard error (SE) of the vegetation height models for both the 6.4km and 18km scale is relatively high (see Table 7). On the other hand, these results generally indicate that on these two scales, vegetation height has a strong positive relationship with the post-fire population dynamics of sage-grouse lek populations, where the higher the percentage of suitable vegetation height surrounding a lek site, the better the population responds to fire. On an 18km scale, vegetation height is a less strong predictor variable, although with an r-squared of 0.12 and a p-value of 0.067, it has a strong tendency towards statistical significance.

Similarly to vegetation height, cheatgrass cover is of great importance in describing the post-fire trend of sage-grouse populations on all three scales. With coefficients of determination (r-squared) of 0.28 (p-value = 0.003), 0.34 (p-value = 0.009) and 0.22 (p-value = 0.01) on a 0.8km, 6.4km and 18km scale respectively, these models explain that there

is a strong negative relationship between the percentage of area with more than 8% cheatgrass cover surrounding a lek site and its post-fire sage-grouse population response. These results help to understand that in the case of this research, vegetation height and cheatgrass cover are two important habitat characteristics that determine the post-fire population trend of sagegrouse lek populations.

Table 7: Univariate model selection summary for different habitat variables influencing post-fire sage-grouse population trends in south-eastern Oregon (2001-2014). Per habitat variable, the spatial scale is sorted from smallest to largest spatial scale. Presented are p-value, r-squared, number of input variables (K), sample size (n), regression coefficients (β) , Akaike Information Criterion (AIC) and Standard Error (SE).

Model	P-Value	R-Squared	K	n	β	AIC	SE
Unburned Area	ı	1	İ	İ	1		1
0.8km Scale	0.07103	0.12	2	29	0.31	26.22	0.16
6.4km Scale	0.28720	0.04	2	29	0.27	28.55	0.25
18km Scale	0.29706	0.04	2	29	-0.45	28.60	0.42
Vegetation Types	ı	1	1	1			1
0.8km Scale	0.03037	0.16	2	29	0.39	24.66	0.17
6.4km Scale	0.15210	0.07	2	29	0.39	27.55	0.27
18km Scale	0.92895	0.00	2	29	0.04	29.78	0.45
Vegetation Cover	ı	1	İ	İ	1		1
0.8km Scale	0.67619	0.01	2	29	-0.25	29.60	0.59
6.4km Scale	0.17209	0.07	2	29	0.44	27.75	0.31
18km Scale	0.19373	0.06	2	29	-1.01	27.94	0.76
Vegetation Height	ı	1	1	1			1
0.8km Scale	0.00017	0.41	2	29	2.88	14.30	0.66
6.4km Scale	0.00008	0.44	2	29	6.35	12.80	1.37
18km Scale	0.06699	0.12	2	29	3.62	26.12	1.90
Cheatgrass Cover	ı	1	İ	İ	1		1
0.8km Scale	0.00292	0.28	2	29	-0.50	20.10	0.15
6.4km Scale	0.00094	0.34	2	29	-0.68	17.82	0.18
18km Scale	0.01703	0.22	2	29	-0.68	22.67	0.25
Distance to Mesic Resources	i	i	İ	Ī	i	1	1
0.8km Scale	0.46872	0.02	2	29	0.12	29.21	0.17
6.4km Scale	0.52249	0.02	2	29	0.15	29.34	0.23
18km Scale	0.83736	0.00	2	29	-0.06	29.74	0.30

After vegetation height and cheatgrass cover, less important habitat predictor variables include vegetation types and unburned area, where the regression models on the 0.8km scale best explain the relationship with the post-fire sage-grouse population. With an r-squared of 0.16 and a p-value of 0.03, vegetation type has a significant positive relationship with the post-fire population trend on a 0.8km-scale at the 95% confidence level, indicating that the higher the percentage of suitable vegetation types surrounding a lek site, the better its persistence and recovery is after a fire. Unburned area performs less well in explaining the post-fire population trend, but on a 0.8km scale, has an r-squared of 0.12 and a p-value of 0.07, indicating that its positive relationship with the post-fire population trend is near statistical significance at the 0.95% confidence level. These results show that on a small scale (0.8km), which is known to affect sage-grouse nesting habitat selection (Walker et al., 2007), the amount of unburned area and presence of suitable species for nesting and breeding surrounding a lek site are related to the post-fire population trend of these lek populations.

Lastly, it can be seen that from all habitat predictor variables, vegetation cover and distance to mesic resources perform very badly in their respective models. For both variables, the models at all scales poorly explain the post-fire sage-grouse population trend, and concluding, no relationship between these variables and the post-fire population trend exist based on these analyses. This is unexpected, since it is hypothesized that these variables have a positive influence on the recovery of sage-grouse lek populations as they are important vegetation and landscape characteristics in the habitat selection of sage-grouse.

4.2.2 Multiple Linear Regression Analysis

Using the results of the univariate regression analysis, the best fit parameters of each scale for the multiple regression analysis were retrieved. The final model set used for the multiple regression analysis can be seen in Table 8 and consisted of the following input variables: unburned area, vegetation types, and distance to mesic resources at a 0.8km scale and vegetation cover, vegetation height and cheatgrass cover on a 6.4km scale. The summary statistics of this model can be seen in model number 4 in Table 9. The values of this final model dataset were converted to z-scores to allow for standardization of different units.

Table 8: Model estimates of standardized (z-score) regression coefficients (β) and standard errors (SE), confidence intervals (Lower and Upper CI) and p-value for effects of habitat variables on the post-fire sage-grouse population trend in south-eastern Oregon (2001-2014). ^a Numbers refer to the radius (km) around a lek site at which the HSP was measured.

Variable ^a	β	SE	Lower CI	Upper CI	P-Value
Vegetation Types 0.8	0.207	0.178	0.29	0.385	0.255
Vegetation Cover 6.4	-0.152	0.215	-0.367	0.063	0.487
Vegetation Height 6.4	0.489	0.171	0.318	0.660	0.009
Cheatgrass Cover 6.4	-0.412	0.239	-0.651	-0.173	0.098
Distance to Mesic Resources 0.8	-0.022	0.166	-0.188	0.144	0.899

The model estimates (Table 8) of the multiple linear regression analyses indicate that the percentage of suitable vegetation height and unsuitable cheatgrass cover at the 6.4km scale have the strongest positive and negative effect respectively on the post-fire population trend of lek sites. On the other hand, vegetation types, vegetation cover and distance to mesic resources poorly explain the post-fire population trend of the analysed lek populations.

For this reason, a stepwise regression was performed to omit redundant input habitat variables. Additionally, assessing for multicollinearity using the variance inflation factor yielded no evidence of multicollinearity. All VIF values were below 3.71, whereas model input variables with VIF values of higher than 10 are usually indicative of severe multicollinearity (O' Brien, 2007). Model parameter selection of the stepwise regression was therefore fully based on AIC values (Table 9).

Table 9: Model selection summary to explain post-fire sage-grouse population trend in relation to habitat features in south-eastern Oregon (2001-2014). Presented are the model input variables, number of input variables (K), sample size (*n*), AIC, R-squared and P-value.

No.	Model Input	K	n	AIC	R- Squared	P- Value
1	Vegetation Height + Cheatgrass Cover	2	29	65.706	0.5564	0.00003
2	Vegetation Types + Vegetation Height + Cheatgrass Cover	3	29	65.889	0.5834	0.00006
3	Vegetation Types + Vegetation Cover + Vegetation Height + Cheatgrass Cover	4	29	65.900	0.6110	0.00010
4	Vegetation Types + Vegetation Cover + Vegetation Height + Cheatgrass Cover + Distance to Mesic Resources	5	29	67.862	0.6115	0.00033

By running a stepwise regression multiple times while assessing the AIC values, it was found that a model containing only vegetation height and cheatgrass cover at the 6.4km scale is most parsimonious. This model explains that vegetation height and cheatgrass cover have the strongest relationships, and that the more suitable the percentage of vegetation height and cheatgrass cover surrounding a lek are on a 6.4km scale, the better a population recovers from a fire.

Figure 12 shows a scatter plot including the regression line for both vegetation height and cheatgrass cover at the 6.4km scale, based on the model estimates from Table 8. In the case of vegetation height, the scatterplot shows three obvious outliers, in which the percentage of suitable vegetation height surrounding these lek sites, as well as the exponential post-fire population trend is notably higher than the other lek sites. The characteristics of these three lek sites will be therefore be discussed in more detail in the discussion section of this research.

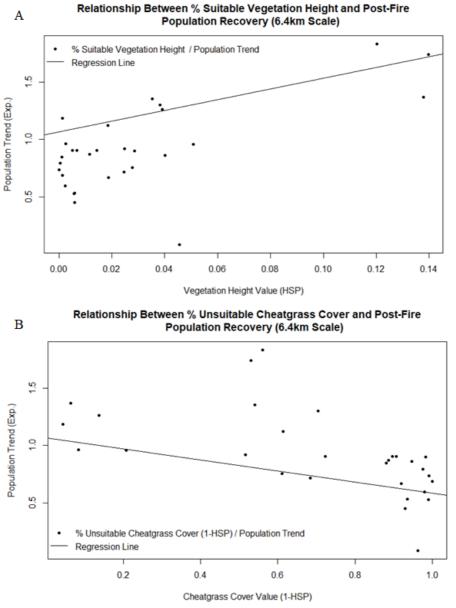


Figure 12: Relationship between percentage area with (A) suitable vegetation height and (B) unsuitable cheatgrass cover and the post-fire population recovery surrounding lek sites at the 6.4km scale at 29 lek sites in south-eastern Oregon. These figures show a positive relationship between the percentage of suitable vegetation height and the post-fire population trend, and a negative relationship between the percentage of unsuitable cheatgrass cover and the post-fire population trend.

4.2.3 Mean Habitat Differences

To assess the habitat characteristics surrounding unburned island lek sites in comparison to fire perimeter lek sites, mean difference tests were conducted to evaluate if there are significant differences between the HSP values of these lek site categories at multiple scales. This was done to assess if besides the general trend between habitat characteristics and the post-fire population trend of lek populations, unburned island lek sites have a higher proportion of suitable vegetation characteristics surrounding their lek sites as compared to fire perimeter lek sites. This may explain their dissimilar lek population response to fire, which is one of the main hypotheses and research questions of this study.

0.8km Scale

At the 0.8km scale, mean difference tests between the HSP values of vegetation cover, cheatgrass cover and distance to mesic resources resulted in no significant differences. The results of this can be seen in Figure 13. The lack of difference with vegetation cover is unexpected, considering it is hypothesized that an increase in the proportion of area with suitable vegetation cover would be a determinant in the persistence of individual sage-grouse and juveniles. However, with a p-value of $0.0579 \, (W = 29.5)$, the mean test results show that the difference in HSP of the distance to mesic resources variable is only marginally failing to be significant at the 95% confidence level. This may indicate that in some way, the presence of mesic resources at small scale (0.8km) may be related to the presence and functioning of unburned islands. However, assessing this in detail was out of the scope of this research.

On average, unburned island lek sites have 39% unburned area surrounding the lek site at the 0.8km scale, whereas unburned area around fire perimeter lek sites is only 12% on average. This indicates the potential importance of a minimum percentage of unburned area surrounding a lek site to function as wildfire refugia in which populations can persist. In addition, vegetation types and vegetation height HSP values are significantly higher around unburned island lek sites as compared to fire perimeter lek sites when using a 95% confidence level. Post-fire percentage of suitable vegetation types for unburned island lek sites is on average 37% versus 7% at fire perimeter lek sites, showing that on average near all remaining unburned vegetation (95%) at unburned island lek sites is suitable vegetation for sage-grouse.

In summary, the results on the 0.8km scale support the hypothesis that an increase in suitable habitat surrounding lek sites leads to an increased post-fire population trend. Furthermore, the results indicate that a minimum amount of suitable habitat surrounding these lek sites may be needed for these areas to function as wildfire refugia in which populations can persist, and that simply the location of a lek site inside of unburned islands may not be enough.

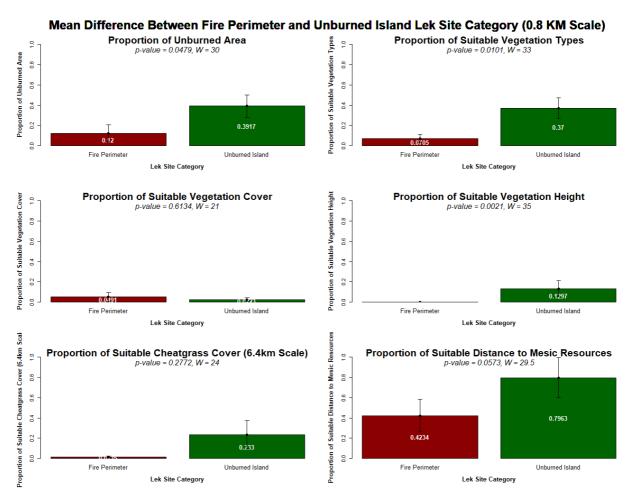


Figure 13: Mean differences for all habitat variables between the HSP of unburned island lek sites and fire perimeter lek sites on a 0.8km scale. These bar graphs show for every habitat variable that was analysed, the average percentage of suitable area surrounding both fire perimeter and unburned island lek sites at this specific spatial scale, as well as if there is a significant difference in the vegetation characteristics or not. Sample size for each lek site category: 7 for fire perimeter and 5 for unburned islands. Test statistics of mean difference tests within each lek site category are shown above each bar graph. Error bars show Standard Error (SE).

6.4 And 18km Scale

Figure 14 shows that at the 6.4km and 18km scale, the mean differences in the HSP values of habitat variables of unburned island and fire perimeter lek sites become less apparent. On these two spatial scales, the only significant difference in HSP surrounding fire perimeter and unburned island lek sites can be found with the habitat variable cheatgrass cover, where percentage area with less than 8% cheatgrass cover is significantly higher surrounding unburned island lek sites as compared to fire perimeter lek sites (6.4km scale: p-value = 0.0160, t = 2.9365, df = 9.2912; 18km scale: p-value = 0.0479, W = 30). At the 6.4km scale, percentage area with suitable cheatgrass cover is 24% as compared to 7% surrounding fire perimeter lek sites. Furthermore, at the 18km scale, percentage area with suitable cheatgrass cover is 37% surrounding unburned island lek sites as compared to 22% at fire perimeter lek sites. These results indicate that cheatgrass cover as a habitat characteristic may partially determine post-fire recovery and persistence of sage-grouse populations even on very large spatial scales such as 18km in this research. This is an interesting finding, as cheatgrass is an important landscape scale habitat component in sagebrush ecosystems. For this reason, these findings will be discussed in more detail in the discussion chapter of this research.

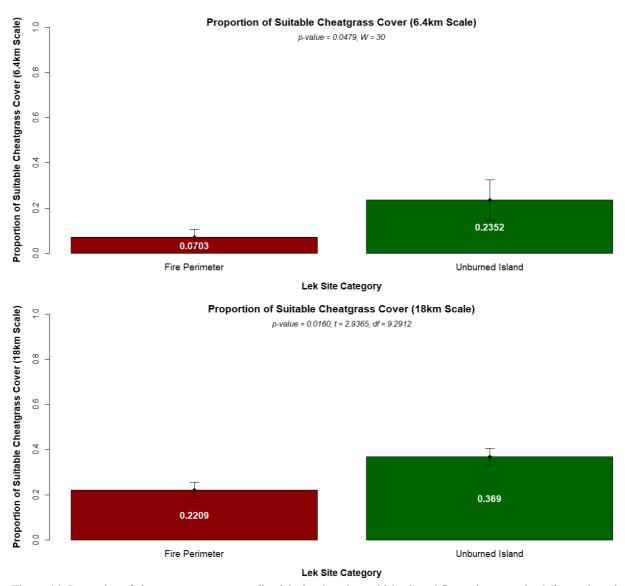


Figure 14: Proportion of cheatgrass cover surrounding lek sites in unburned islands and fire perimeter at the 6.4km scale and 18km scale. This figure shows at the 6.4km scale and 18km scale the average proportion of the area surrounding the lek sites which has less than 8% cheatgrass cover (suitable). It can be seen that at both scales, unburned island lek on average have a significantly higher percentage of suitable cheatgrass cover as compared to fire perimeter lek sites. Sample size for each lek site category is: 7 for fire perimeter, 5 for unburned island. Test statistics of mean difference tests within each lek site category are shown above each bar graph. Error bars show Standard Error (SE).

5. Discussion

This research performed one of the first in-depth examinations of the effect of spatial distribution of sage-grouse lek populations on their population response to fire disturbances. Furthermore, it is one of the first studies to evaluate the effect of unburned islands and their habitat characteristics on the post-fire population trend of sage-grouse lek populations. In the following three paragraphs, the results of these analyses will be discussed using the hypotheses of this research. Afterwards, the broader implications of the research findings on fire refugia will be argued.

5.1 Negative Effects of Fire on Sage-Grouse Lek Populations

Consistent with the first hypothesis of this research, the results of this study show that sage-grouse populations in south-eastern Oregon are negatively affected by fire if their respective lek sites are located inside of the fire perimeter. Based on previously conducted research, most of these results may be attributed to several factors related to the life traits and ecological requirements of sage-grouse.

Some of the main factors that may explain why it can be seen that these sage-grouse lek populations respond negatively to fire is that sage-grouse exhibit strong site fidelity to natal lek sites (Dunn and Braun, 1985), have low emigration rates (Doherty et al., 2010; Foster, 2016) and require widespread and intact sagebrush during all stages of their life (Crawford et al., 2004; Connelly et al., 2011b). Consequently, at the population level, sagegrouse may continue to select resources and habitat within fire-affected seasonal ranges (Connelly et al., 2011b), even if it leads to loss of fitness and reduced nesting success and survival of juveniles (Van Horne, 1983; Fischer et al., 1993). This pattern is supported by research from Foster (2016), who found that sage-grouse occupying burned areas suffered acute and lasting fitness loss during at least the first two years after the fire, where survival of both adults and vearling sage-grouse was consistently low. Additionally, nesting success on burned lek sites in the year after fire was 19%, which is amongst the lowest reported for sagegrouse (Foster, 2016), as previously documented nesting success in healthy sagebrush habitat ranges between 15%-86% and is often greater than 40% (Connelly et al., 2000b; Connelly et al., 2011b). Low nesting success and survival in burned areas is possibly caused by increased predation from birds of prey such as common ravens (Corvus corax), who are known to be one of the primary causes of sage-grouse mortality (Hagen, 2011b), as well as food stress during winter (Foster, 2016). Especially in burned areas, where lack of vegetation offers less to no protective cover from avian predators, predation of sage-grouse eggs and juveniles may be a major limiting factor for sage-grouse population persistence after fire (Connelly et al., 1991, Gregg et al., 1944). The lack of suitable amount of vegetation for nesting, breeding, cover and food for lek populations within the fire perimeter was supported by the results of the habitat composition and suitability analyses. These results showed that on average, only 12% of the area surrounding lek sites in the fire perimeter remained unburned after fire at the 0.8km scale, largely reducing the carrying capacity of the landscape.

In short, the population declines of sage-grouse lek populations within the fire perimeter that were observed during this study may potentially be attributed to a combination of high philopatry to lek sites and lack of suitable remnant habitat surrounding these lek sites which is required for nesting, breeding, food and cover. These may also be some of the factors

that may explain why fire perimeter lek site populations show such a dissimilar response to fire as compared to lek populations within unburned islands and outside of the fire perimeter.

5.2 Unburned Islands as Wildfire Refugia for Sage-Grouse

In contrast to fire perimeter lek populations, the results from this study showed that lek populations with lek sites situated inside of unburned islands were not significantly negatively affected by fire, and their populations even increased on the long-term, despite the fact that the average population declines slightly in the first 5 years after fire. This is according to hypothesis one, which argues that unburned island lek populations are not negatively affected by fire because these areas may function as wildfire refugia. The persistence of sage-grouse lek populations within unburned islands may be caused by several factors.

Some factors that may explain why it can be observed that sage-grouse lek populations in this research persist in unburned islands is that unburned islands preserve key habitat functioning (Robinson et al., 2013), as well as that the post-fire distribution of unburned islands may possess several characteristics that enhance survival and recovery of sage-grouse (Longland and Bateman, 2002). For instance, unburned islands largely retain their capability to provide cover from predation, which notably affects nesting success and survival (Wallestad and Pyrah, 1974; Gregg et al., 1994), as well as continuing to offer a direct food source for sage-grouse. In burned areas, the post-fire abundance of Hymenoptera (ants, wasps and bees), Coleoptera (beetles) and edible sagebrush reduces significantly as compared to unburned areas (Rickard, 1970; Fisher et al., 1996; Pyle and Crawford, 1996; Rhodes et al., 2010). This is critical, as sagebrush and insects are one of the most important sources of food in the diet of both young and adult sage-grouse (Patterson, 1952; Miller and Eddleman, 2000).

The findings of this research also support the hypothesis that unburned islands may allow for the persistence of sage-grouse lek populations through functioning as wildfire refugia. It was found that at a 0.8km scale, unburned island lek sites have significantly higher percentages of unburned area (39% vs 12%), suitable vegetation types and vegetation height, which may be a major determinant in the persistence of these lek populations after fire.

5.3 The Effect of Habitat Suitability on Post-Fire Population Response

From the results of this research, it was observed that in several cases, there is a strong relationship with the post-fire habitat characteristics and suitability and the post-fire population trend of lek populations. At the 0.8km scale, an increase in the proportion of suitable vegetation types surrounding a lek site, and at the all spatial scales, an increase in the proportion of suitable vegetation height and decrease in cheatgrass cover resulted in a better population response to fire. Additionally, unburned island lek populations have a considerably higher amount of unburned area, proportion of suitable vegetation types and vegetation height surrounding their respective lek sites at the 0.8km scales as compared to fire perimeter lek populations. This is in line with hypothesis two of this research, which suggests that sagegrouse lek populations perform better after fire when the amount of suitable post-fire habitat surrounding lek sites increases.

This positive response of sage-grouse lek populations to an increase in suitable habitat surrounding their lek sites at the 0.8km scale may be explained by the species' high site fidelity and requirements for intact sagebrush. For example, sage-grouse hardly move farther

away than 1km from leks during nesting and breeding season (Wallestad and Schladweiler, 1974), and sage-grouse hens may nest within <200 of previous year's nests at the same lek site (Gates, 1983). Moreover, during the breeding season, Foster (2016) found that sage-grouse selected for locations with 100% intact sagebrush within a range of 1km² around a lek site. Lastly, sage-grouse require tall sagebrush stands for food and cover in winter, when available sagebrush is often restricted severely because of snow depth (Hupp and Braum, 1989), and avoid cheatgrass due to unsuitability as a source of food and cover (Crawford et al., 2004). For these reasons, suitable unburned habitat at small scale is of special importance to sage-grouse and may therefore explain the positive relationship with post-fire population response of lek populations.

At the 6.4km and 18km scale, proportion of suitable vegetation height and cheatgrass cover appeared to be important model parameters, with a strong positive and negative effect respectively on the post-fire trend of lek populations. It is especially interesting that cheatgrass cover is strongly related to the post-fire population trend of sage-grouse at all spatial scales. This may be related to several factors. First, presence of cheatgrass is often related to anthropogenic disturbances and human development, which sage-grouse strongly avoid (Johnson et al., 2011; Kirol et al., 2012). Thus, sage-grouse may avoid such areas on a larger scale not only because they contain unsuitable amount of cheatgrass, but also because these areas are situated near anthropogenic disturbances (Naugle et al., 2011). Second, presence and invasibility of cheatgrass in the Great Basin is strongly related to climatological gradients, such as elevation, temperature and precipitation (Chambers et al., 2007). As a result, lek populations with lower cheatgrass cover surrounding their lek sites may therefore respond better to fire because these areas are generally higher elevated, wetter and colder, which may make these lek populations and their surroundings inherently more resilient to disturbances (Chambers et al., 2014). Additionally, wetter and higher elevated areas are naturally more suitable to sage-grouse, because they have a higher plant productivity, longer growing season, and higher forb and insect abundance, which offer excellent sources of food and cover as compared to lower elevated xeric areas (Dunn and Braun, 1986; Drut et al., 1994b). This in term may also explain why the lek populations with higher percentage of suitable vegetation height surrounding their lek sites respond better to fire.

In the model of vegetation height, three lek sites ("Dry Creek N2", "Opal Reservoir N1" and "Pretty Rock Reservoir") were particularly important in determining the strong positive relationship with post-fire population response. These lek sites had a post-fire population trend of 1.83, 1.74 and 1.37 respectively. After assessing for mean differences using a two paired t-test it was found that these three lek sites are located at a significantly higher elevation than the other sites, with an elevation of 1834m, 1742m and 1681m respectively versus a mean elevation of 1457m for the other lek sites (p-value = 0.002, t = 0.5014, df = 5.7964). This could mean that these populations may respond better to fire because they are located inside of more resilient areas to disturbances. However, evaluating the effects of climatological conditions and resilience to disturbances on the post-fire response of lek populations was out of the scope of this research.

Lastly, secondary analyses were performed without outliers to assess if similar univariate and multiple regression analyses without these values would yield in different results. The dataset of post-fire population trend contained three outliers, namely the: "Dry

Creek #2", "Opal Reservoir N1" and "Fields Creek" lek sites, with an exponential post-fire population trend of 1.83, 1.74 and 0.08 respectively. It was observed that when performing regression analyses without these three outliers, some significant changes were present in the results. First, no relationship exists anymore between the proportion of suitable vegetation height and the post-fire population trend at the 0.8km scale. However, at the 0.8km scale, there is now a significant relationship with proportion of unburned area and the population trend, as well a significant relationship with the proportion of suitable vegetation types and vegetation cover at the 6.4km scale. For the rest, results did not differ meaningfully, as the most parsimonious model in the multiple regression without outliers also consisted of vegetation height and cheatgrass cover at the 6.4km scale as the two remnant habitat variables.

5.4 Broader Implications for Wildfire Refugia

In the research field of refugia, a major knowledge gap exists in the understanding of the postfire dynamics of wildlife species within unburned islands. Therefore, there is a great need to understand what constitutes refugia for a particular species, as well as to identify relationships between life-history attributes of species and their need for and use of unburned islands (Robinson et al., 2013). This is amplified because refuges for wildlife species are becoming increasingly important under the expected changes in fire frequency, size and severity (McKenzie et al., 2004), which may reduce unburned islands (Abatzoglou and Williams, 2016).

The results of this research show that in the case of a high philopatry species like the sage-grouse, which generally are at higher risk of mortality by fire (Robinson et al., 2013), unburned islands may completely mitigate the negative effects of fire disturbances. This is a finding of ecological importance which may assist in conservation planning for sage-grouse populations that are subject to fire by showing the need to protect and potentially create and enhance unburned islands in and around critical habitat of known lek populations. Additionally, the results of this research increase general understanding of the ecological function of unburned islands for wildlife species by showing that unburned islands may allow for the persistence of wildlife species during and after fire. This information may be used to try and understand the effects of unburned islands on the post-fire dynamics of other wildlife species in both sagebrush and other fire-prone ecosystems around the world.

6. Synthesis and Conclusion

6.1 Summary of Key Findings

Sage-grouse lek populations in this study were all subject to large scale fire in or surrounding their lek sites at some point during the period 1984-2014. First, the effect of the spatial distribution of lek populations to these fire disturbances was looked at. Lek sites were subdivided into four different lek site categories: fire perimeter, unburned island, inner buffer (0-1500m) and outer buffer (1500-6400m). It was found out that sage-grouse lek populations that have their lek site located inside of the fire perimeter are negatively affected by fire up to the point where these populations on average nearly completely eradicate in the first five years after fire. Because sage-grouse have high site fidelity, the population declines that can be observed following wildfire in this study are most likely due to reduced sage-grouse survival in the years after fire through loss of carrying capacity of the landscape. Sage-grouse lek populations that had their lek site located inside of unburned islands were not significantly affected after fire, and even increased in several cases. Surprisingly, lek populations with lek sites located outside but near the fire perimeter were also in some cases affected equally by fire disturbance as those inside of the fire perimeter. These results indicated that the post-fire habitat composition surrounding lek sites is plausibly a major determinant in the persistence and recovery of sage-grouse lek populations after fire.

For this reason, the post-fire habitat composition surrounding lek sites was modelled. Afterwards, the relationship between the post-fire habitat composition surrounding lek sites and the post-fire response of their respective sage-grouse lek population was assessed at multiple scales. Specifically, the impact of unburned area, vegetation type, cover and height, as well as cheatgrass cover and distance to mesic resources were modelled because these are habitat characteristics that are known to play a major role in the habitat selection of sagegrouse. These habitat suitability models were converted to a metric of HSP, which represented the percentage of unburned area surrounding the lek site at each spatial scale. The results of these analyses suggest that there is a positive relationship between the percentages of suitable vegetation types and vegetation height surrounding a lek site and its' population response to fire at the 0.8km and 6.4km scale respectively. In the case of cheatgrass cover, there is a strong negative relationship between the proportion area with unsuitable cheatgrass cover and the post-fire population trend at the 6.4km scale. Furthermore, it was found that lek sites inside of unburned islands had a significantly higher percentage of unburned area (39% versus 12%), suitable vegetation types (37% versus 5%) and suitable vegetation height (13% versus 0%) at the 0.8km scale as compared to lek sites located inside of the fire perimeter. Presumably, the disproportionately higher amount of unburned area and suitable vegetation surrounding unburned island lek sites at small scale is a major determinant in causing their dissimilar population response to fire as compared to fire perimeter lek sites.

6.2 Management Implications

Because of the high site fidelity of sage-grouse to their natal lek sites and seasonal and home ranges (Dunn and Braun, 1985; Connelly et al., 2011), as well as the fact that sage-grouse continue to utilize disturbed habitat surrounding their lek sites following large-scale wildfire (Foster, 2016), it is suggested that management actions should be undertaken to preserve

sage-grouse habitat in the direct vicinity of known active lek sites. This is supported by the results of this research, which indicate that sage-grouse lek populations can persist and recover better from fire if the small-scale habitat surrounding their respective lek site is maintained, such as in the case of unburned islands within a fire perimeter. Small-scale habitat surrounding lek sites (0.8km radius) can therefore be seen as a priority area of conservation for sage-grouse populations. However, management of these areas would require consideration of the ecological requirements of sage-grouse in the context of their whole ecosystem (Murphy et al., 2013). Because of this, several recommendations are made that are targeted towards prioritizing and implementing conservation efforts at the places and scales where they are most needed and most likely to be successful.

First, as sage-grouse are true sagebrush obligates (Crawford et al., 2004), and sagebrush requires long periods of between 20-50 years to recover from fire (Nelle et al., 2000; Lesica et al., 2007), it is suggested that pre-fire efforts are undertaken to inhibit the spread and size of wildfires in known sage-grouse habitat at landscape scale. This includes treatment of invasive and encroaching species like cheatgrass and juniper into sage-grouse habitat, which are known to both compete with sagebrush for space and alter fire regimes negatively by creating larger and more severe fires with detrimental effects on sage-grouse ecosystem health (Miller et al., 2011; Miller et al., 2013). Furthermore, attempts need to be made to use fire-breaks at multiple scales to ensure that individual fires do not reach disastrous sizes, as well as that priority sage-grouse habitat is protected from fire (Murphy et al., 2013). This is in line with the conservation plan of the Western Association of Fish and Wildlife Agencies, who propose to establish defensible fire lines in carefully selected locations of importance to sage-grouse (Murphy et al., 2013). By doing so, perimeters can potentially be constructed around known active lek sites so that in the case of fire, unburned islands of suitable size can be formed that allow for the persistence of their lek populations. Due to the strong selection of sage-grouse for intact and high quality sagebrush during nesting, breeding and wintering habitat (Gregg et al., 1994; Connelly et al., 2000), managers should also strive to maintain suitable vegetation characteristics of these unburned islands. Although little is known about the sage-grouse population response to large-scale restoration projects in wintering and nesting habitat, judicious use of small-scale vegetation treatments may be a viable conservation practice to enhance these small-scale sage-grouse habitat patches where possible (Dahlgren et al., 2006; Taylor et al., 2011).

Due to increase fire activity in the future, fire prevention and suppression are most likely not the ultimate solutions to prevent the unwanted changes caused by fire in sagebrush ecosystems (Miller et al., 2011). Consequently, long-term land management actions need to be designed that can improve the resilience of sagebrush ecosystems to fire disturbances (Murphy et al., 2013; Chambers et al., 2014). For this reason, increased knowledge about the ecological importance of fire resilient areas like unburned islands on the persistence of sagegrouse lek populations as retrieved from this research is potentially vital information for the development of future wildfire management plans in the Great Basin.

6.3 Suggestions for Future Research

In the past, research on the effects of fire on sage-grouse populations was more concerned with the habitat alterations in sage-grouse habitat after fire. Only recently did researchers start to examine the demographic response of sage-grouse populations to fire disturbances, and a general negative trend is observed for many lek populations throughout their whole range (Coates et al., 2015). However, the consequences of wildfire on sage-grouse populations are presently not fully understood, partially because the relationship between the sage-grouse population trend after fire and post-fire habitat composition and habitat selection is underresearched. On top of this, many studies have erroneously excluded and ignored unburned islands from fire research, and as a result, the characteristics and large-scale ecological importance of unburned islands remain largely unknown to date (Kolden et al., 2012). Accordingly, this study combined both unburned islands and post-fire habitat composition around lek sites and assessed their characteristics in relation to the response of sage-grouse lek populations. This is an innovative approach to understand the potential consequences of wildfire on sage-grouse populations and habitat. However, because it is an innovative approach, several interesting findings and research ideas were out of the scope of this research. Furthermore, multiple methodological decisions had to be made that may have impacted the accuracy of the research.

For example, expanding the study area to the whole range of sage-grouse might reveal if the results of this research apply for sage-grouse populations throughout their whole range in the Great Basin. Additionally, it would notably increase the sample size, which is arguably one of the main stumbling blocks of this research. Utilizing datasets with longer time periods of fire perimeters than 17 years in this research may also more accurately represent the past burned and unsuitable area for sage-grouse in the landscape, because sagebrush ecosystems normally require more than 17 years to recover up to the point where it is suitable for sage-grouse. This was a limitation in this research that may have reduced the accuracy of the post-fire habitat composition surrounding each lek site.

Additionally, only three spatial scales of 0.8km, 6.4km and 18km were used to assess post-fire habitat composition surrounding lek sites and their effect on the post-fire population trend of their lek populations. By performing these analyses for an additional amount of spatial scales between the scales of 0.8km and 18km, it can potentially be found out if the post-fire population trend can be explained better if the habitat suitability is modelled at a smaller or larger spatial scale than has been done in this research.

Besides the use of longer periods of fire perimeters, modelling recovery in these burned areas might be important in improving model accuracy and reliability. In the case of this research, if an area was burned in the 17 years before the fire, it was categorized as unsuitable. However, in reality, burned areas within the fire perimeter recover up to the point where some vegetation types such as forbs and grasses recover quickly and can be utilized by sage-grouse for post-fire recovery in the form of food and cover (Beck et al., 2009; Foster, 2016). By including temporal recovery of burned habitat surrounding lek sites, rather than labelling it as unsuitable over the whole period of 17 years in the case of this study, this might improve the models' ability to realistically explain the post-fire population trend of the lek populations.

Furthermore, instead of using relatively crude datasets from both LANDFIRE and a dataset of hydrological features, it would potentially be more accurate and realistic to utilize a map of actual mesic resource, as well as to construct own maps of vegetation characteristics based on for example satellite imagery from Landsat or LiDAR, and to verify these characteristics using field surveys. By doing so, vegetation characteristics like height, type and cover may then be represented on a higher resolution, in which small-scale habitat features which are important to sage-grouse habitat selection may more easily be distinguished.

Lastly, the results of this research showed that several lek sites with a good response to fire had suitable habitat characteristics and were located in significantly higher elevated areas than the other lek sites. This could indicate that response to disturbances may also be related to climatological conditions and resilience to disturbances such as fire and invasion of exotic species. Assessing this in more detail may yield in interesting results regarding the effect of mesic and higher elevated areas as resilient habitat for wildlife species.

Concluding, this research proved to be an excellent opportunity to utilize the relatively newly created unburned islands database from Meddens et al. (2016) to assess the ecological importance of unburned islands in the conservation of wildlife species such as the sage-grouse. Even with a small sample size and relatively crude datasets of vegetation characteristics, this study proved to show a significant relationship between the small-scale post-fire habitat composition surrounding burned lek sites and their sage-grouse population recovery and persistence, which is a finding of importance to the long-term management of sage-grouse populations in the Great Basin. Besides, this research contributed to increased knowledge about the ecological functioning of unburned islands in the persistence of high philopatry species such as sage-grouse. This information may be used to guide future research regarding the effects of refugia on wildlife species in sagebrush and other ecosystems that are prone to fire.

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7.1 Figures

Figure 1: (Left) Retrieved from

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Figure 1: (Right) Retrieved from

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Figure 2: (Left) Retrieved from

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Figure 2: (Right) Retrieved from

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8. Appendices

Appendix A1: Population trends before and after fire for each lek site and lek site category, including the p-value for the mean difference test between each lek site, as well as the year of fire.

Fire Perimeter Lek Sites

Lek Site	P-Value	Slope Before Fire	Slope After Fire	Fire Year
"FIELDS_CREEK"	0	1,114	0,083	2006
"MERRILL"	0,018	0,958	0,736	2012
"JACK MOUNTAIN N4"	0,002	0,993	0,687	2012
"DOWNEY_CREEK"	0,006	1,008	0,667	2012
"JACK_MOUNTAIN_N2"	0,037	0,947	0,597	2012
"DOG_CREEK"	0	1,078	0,453	2007
"SCHURTZ_FIELD"	0	1,105	0,905	2007

Unburned Island Lek Sites

Lek Site	P-Value	Slope Before Fire	Slope After Fire	Fire Year
"DRY_CREEK_N2"	0	1,066	1,834	2012
"OPAL_RESERVOIR_N1"	0	1,005	1,741	2012
"FIELDS_BASIN"	0	1,107	0,862	2006
"COLD_N1"	0	1,046	0,846	2006
"HANNA_N1"	0,001	1,061	0,904	2012

Inner Buffer Lek Sites

Lek Site	P-Value	Slope Before Fire	Slope After Fire	Fire Year
"EGLI_RIM_NORT	0	1,015	0,716	2002
Н"				
"WHISKEY_SPRIN	0,003	1,026	0,965	2006
GS_N1"				
"RICKMAN_SPRIN	0	1,029	1,303	2012
G_N2"				
"LARRY_S"	0	1,001	0,529	2012
"FOLLY_FARM"	0	0,982	0,905	2001
"THIRSTY_HOG"	0,001	1,06	0,535	2007

Outer Buffer Lek Sites

Lek Site	P-Value	Slope Before Fire	Slope After Fire	Fire Year
"THE_GAP_ROAD	0	0,987	1,263	2006
"				
"MAUPIN_SPRING	0	0,882	1,007	1998
_N1"				
"HUMBOLDT_RID	0	0,84	1,357	2012
GE_SOUTH"				
"HILLTOP_N1"	0	0,97	0,909	1999
"BLIZZARD_N2"	0	0,945	1,095	1999
"FLOOK_BURN"	0	1,04	1,185	2010
"TRAINER_PLAYA	0,003	1,007	0,795	2012
_N2"				
"LONE_PINE_ROA	0,047	1,065	0,958	2010
D"				
"LONG_DAM"	0,001	0,982	1,002	1997
"HOUSE_BUTTE_	0	0,963	1,121	2007
N4"				
"PRETTY_ROCK_	0	1,073	1,371	2012

RESERVOIR"				
"ROY_RESERVOI	0,01	1,14	0,899	2014
R"				
"VIRTUE_N2"	0	0,998	0,921	2001
"WATER_TROUG	0	1,379	0,841	1998
Н"				
"EAST_WIDMAN"	0	1,053	0,754	2012
"STICKY_JOE_N1"	0	1,088	0,87	2007

Appendix A2: Habitat Suitability Percentages for Each Lek Site at the 0.8km scale

Lek Site	Slope Afte r Fire	Habitat V alue	Unburned Area	Vegetatio n Types V alue	Vegetatio n Cover V alue	Vegetatio n Height Value	Cheatgras s Cover V alue	Hydrolog y Distance Value
"FIELDS CREEK"	0,0833	0,0064	0,0107	0,0107	0	0	1	0,4596
"MERRI LL"	0,7365	0,0262	0,0437	0,0437	0	0	0,9589	0
"JACK M OUNTAI N N4"	0,6875	0,9006	1,5324	1,378	0,0875	0,0884	0,9786	0,9978
"DOWNE Y CREEK	0,6665	0,041	0,0687	0,0611	0,0071	0	1	0
"JACK M OUNTAI N N2"	0,5971	0,0203	0,0339	0,0339	0	0	1	0,7662
"DOG CR EEK"	0,4527	0,367	0,6301	0,3025	0,3249	0	1	0,9946
"SCHUR TZ FIEL D"	0,9045	0,0337	0,0531	0,0415	0,0116	0	0,9469	0,7434
"DRY CR EEK N2"	1,8343	0,4109	0,5587	0,556	0,0049	0,3061	0,4378	0,9951
"OPAL R ESERVOI R N1"	1,7413	0,4471	0,6162	0,6073	0,0089	0,3378	0,4003	0,9955
"FIELDS BASIN"	0,8625	0,0435	0,0723	0,0723	0	0,0022	0,9969	0
"COLD N 1"	0,8455	0,1119	0,1865	0,1852	0,0018	9e-04	1	0,996
"HANNA N1"	0,9036	0,3132	0,5248	0,4293	0,0959	0,0013	1	0,9951
"EGLI RI M NORT H"	0,7156	0,5575	0,9317	0,9237	9e-04	0,0714	0,9933	0,9978
"WHISK EY SPRI NGS N1"	0,9652	0,5979	0,9973	0,9964	0	0	0,2718	0
"RICKM AN SPRI NG N2"	1,3029	0,5974	0,9929	0,9393	0,0589	0,0013	0,9563	0,996
"LARRY S"	0,5291	0,5987	0,9978	0,9835	0,0143	0	1	0,9978
"FOLLY FARM"	0,9048	0,68	0,9973	0,9746	0	0	0,0585	0,9973
"THIRST Y HOG"	0,5346	0,54	0,9308	0,6774	0,2338	4e-04	1	0,9969
"THE GA	1,2635	0,5992	0,9978	0,9933	0	0,0027	0,0022	0

P ROAD"								
"HUMBO	1,3568	0,6149	0,9781	0,9215	0,1946	0,0228	1	0,9982
LDT RID								
GE SOUT								
H"								
"FLOOK	1,185	0,6494	0,9964	0,9942	0	0	0,0036	0
BURN"			1			_		
"TRAINE	0,7952	0,5976	0,996	0,9822	0,0062	0	1	0,996
R PLAYA N2"								
"LONE P	0,9579	0,5976	0,9942	0,6332	0,3588	4e-04	0,0353	0,9955
INE ROA	0,9379	0,3970	0,9942	0,0332	0,3388	46-04	0,0333	0,9933
D"								
"HOUSE	1,1206	0,5907	0,9955	0,6832	0,2753	0,0013	0,3958	0,9955
BUTTE N								_
4"								
"PRETT	1,3709	0,7921	0,9964	0,9728	0,0071	0,0085	0,0036	0,9964
Y ROCK								
RESERV								
OIR"			1					
"ROY RE	0,8993	0,489	0,8224	0,7938	0,0112	0,0259	0,9714	0,9973
SERVOI R"								
"VIRTUE	0,921	0,6054	0,9955	0,6435	0,3574	0	0,4507	0,8742
N2"	0,921	0,0034	0,9933	0,0433	0,3374		0,4307	0,8742
"EAST W	0,7537	0,5863	0,9652	0,7912	0,178	0,0013	0,7229	0,9996
IDMAN"	.,,,	-,	.,	.,	.,	.,	,,,===	,,,,,,,
"STICKY	0,8697	0,5691	0,9473	0,9268	0,1075	0,0036	1	0,9964
JOE N1"								

Appendix A3: Habitat Suitability Percentages for Each Lek Site at the 6.4km scale

Lek Site	Slope Afte r Fire	Habitat V alue	Unburned Area	Vegetatio n Types V alue	Vegetatio n Cover V alue	Vegetatio n Height Value	Cheatgras s Cover V alue	Hydrolog y Distance Value
"FIELDS CREEK"	0,0833	0,1117	0,1785	0,1761	0,1201	0,0456	0,0369	0,5661
"MERRI LL"	0,7365	0,0075	0,0125	0,0123	0,0075	0	0,0086	0,2846
"JACK M OUNTAI N N4"	0,6875	0,0141	0,024	0,0216	0,0123	0,0014	3e-04	0,9995
"DOWNE Y CREEK "	0,6665	0,3586	0,5939	0,5186	0,1345	0,0188	0,0797	0,3255
"JACK M OUNTAI N N2"	0,5971	0,244	0,4172	0,35	0,2701	0,0023	0,0193	0,6804
"DOG CR EEK"	0,4527	0,4824	0,8124	0,6223	0,4695	0,006	0,0707	0,8503
"SCHUR TZ FIEL D"	0,9045	0,2321	0,376	0,2992	0,1209	0,0051	0,2767	0,7488
"DRY CR EEK N2"	1,8343	0,3091	0,4129	0,3771	0,2358	0,1203	0,4401	0,9995
"OPAL R ESERVOI R N1"	1,7413	0,3559	0,4792	0,4515	0,25	0,1396	0,4701	1
"FIELDS BASIN"	0,8625	0,1132	0,183	0,1774	0,1447	0,0401	0,0524	0,3113

"COLD N	0,8455	0,3408	0,5671	0,5426	0,1577	0,0011	0,1197	0,9324
1"		Í	ĺ	0,5720		ĺ		Í
"HANNA	0,9036	0,3516	0,5834	0,4827	0,1907	0,0142	0,0936	0,9976
N1" "EGLI RI	0,7156	0,4663	0,8106	0,6531	0,3544	0,0246	0,3161	0,7084
M NORT	0,7100	0,1005	0,0100	0,0231	0,5511	0,0210	0,5101	0,7001
Н"	0.0650		0.0714	0.0454	0.0614	0.0006	0.01/0	
"WHISK EY SPRI	0,9652	0,5727	0,9514	0,9454	0,8611	0,0026	0,9162	0
NGS N1"								
"RICKM	1,3029	0,4607	0,7388	0,7215	0,3461	0,0382	0,2951	0,7068
AN SPRI								
NG N2" "LARRY	0,5291	0,4321	0,7212	0,7138	0,2448	0,0057	0,0097	0,92
S"		Í	ĺ	Í		ĺ		Í
"FOLLY	0,9048	0,3419	0,5808	0,4894	0,3286	0,0067	0,1026	0,6946
FARM" "THIRST	0,5346	0,4696	0,787	0,6114	0,4849	0,006	0,0638	0,9965
Y HOG"	0,3340	0,4070	0,707	0,0114	0,707	0,000	0,0036	0,7703
"THE GA	1,2635	0,5366	0,8539	0,8408	0,5563	0,0391	0,8638	0,0954
P ROAD" "HUMBO	1,3568	0,487	0,7616	0,7398	0,4721	0,0353	0,459	0,9952
LDT RID	1,5000	0,107	0,7010	0,7270	0,1721	0,000	0,.05	0,5502
GE SOUT								
H" "FLOOK	1,185	0,6655	0,9919	0,9482	0,8866	0,0012	0,957	0,3123
BURN"	1,100	0,0000	0,5515	0,5 102	0,0000	0,0012	0,557	0,5125
"TRAINE	0,7952	0,5868	0,9834	0,9533	0,4883	5e-04	0,0237	0,8479
R PLAYA N2"								
"LONE P	0,9579	0,4871	0,7772	0,5535	0,2975	0,0509	0,7923	1
INE ROA D"								
"HOUSE	1,1206	0,5267	0,8807	0,6465	0,3318	0,0186	0,3856	0,9973
BUTTE N		,	,	,				,
4" "PRETT	1,3709	0,7082	0,9362	0,8746	0,6894	0,1379	0,937	0,9999
Y ROCK	1,3709	0,7082	0,9302	0,8740	0,0694	0,1379	0,937	0,9999
RESERV								
OIR"	0.0002	0.4624	0.7792	0.6744	0.2476	0.0295	0.0172	0.0250
"ROY RE SERVOI	0,8993	0,4634	0,7782	0,6744	0,2476	0,0285	0,0173	0,9358
R"								
"VIRTUE N2"	0,921	0,4259	0,6555	0,743	0,3166	0,0247	0,4846	0,6472
"EAST W	0,7537	0,5474	0,8426	0,567	0,424	0,0278	0,3891	0,9999
IDMAN"		ŕ				ĺ		Í
"STICKY	0,8697	0,4951	0,8429	0,6654	0,5028	0,0116	0,1129	0,6735
JOE N1"								

Appendix A4: Habitat Suitability Percentages for Each Lek Site at the 18km scale

Lek Site	Slope Afte r Fire	Habitat V alue	Unburned Area	Vegetatio n Types V	Vegetatio n Cover V	Vegetatio n Height	Cheatgras s Cover V	Hydrolog y Distance
				alue	alue	Value	alue	Value
"FIELDS	0,0833	0,4006	0,6673	0,529	0,0191	0,1043	0,3529	0,3474
CREEK"								
"MERRI	0,7365	0,1278	0,2057	0,148	0,0309	0,0108	0,1476	0,1514
LL"								
"JACK M	0,6875	0,2867	0,4717	0,3616	0,0694	0,0405	0,1194	0,3945

OLINITAL			1				1	
OUNTAI N N4"								
"DOWNE	0,6665	0,5167	0,8523	0,6252	0,1707	0,0371	0,2695	0,6579
Y CREEK	0,0003	0,3107	0,8323	0,0232	0,1707	0,0371	0,2073	0,0377
"JACK M	0,5971	0,3869	0,6488	0,4389	0,0959	0,036	0,2558	0,4977
OUNTAI	0,0 > / 1	0,2009	0,0100	0,1507	0,000	0,020	0,200	0,1277
N N2" "DOG CR	0,4527	0,476	0,7952	0,6176	0,2226	0,0184	0,1226	0,6874
EEK"		0,170	,	0,0170	0,2220	0,0101	0,1220	0,0071
"SCHUR TZ FIEL	0,9045	0,4685	0,7825	0,5877	0,1586	0,0183	0,2785	0,8186
D"								
"DRY CR EEK N2"	1,8343	0,3123	0,4165	0,3853	0,0436	0,0955	0,4277	0,4245
"OPAL R	1,7413	0,3377	0,4477	0,4129	0,034	0,0956	0,4824	0,4837
ESERVOI R N1"								
"FIELDS BASIN"	0,8625	0,3671	0,6293	0,4789	0,012	0,0764	0,3142	0,3278
"COLD N	0,8455	0,4705	0,7677	0,6845	0,078	0,0042	0,3336	0,6606
"HANNA	0,9036	0,4939	0,8026	0,6297	0,169	0,0593	0,2873	0,8929
N1" "EGLI RI	0,7156	0,4243	0,7535	0,5168	0,0635	0,0287	0,4804	0,529
M NORT H"	.,.		.,	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	,,,,,,,,,			
"WHISK	0,9652	0,5197	0,8376	0,8489	0,0034	0,0493	0,8805	0,1818
EY SPRI NGS N1"								
"RICKM	1,3029	0,4412	0,7114	0,6475	0,0627	0,0244	0,4975	0,6951
AN SPRI NG N2"								
"LARRY S"	0,5291	0,3795	0,6419	0,5523	0,038	0,0071	0,0905	0,4709
"FOLLY FARM"	0,9048	0,4316	0,7216	0,6515	0,045	0,0246	0,1229	0,6452
"THIRST	0,5346	0,5116	0,8456	0,6742	0,2276	0,0251	0,1698	0,742
Y HOG" "THE GA	1,2635	0,4336	0,6985	0,7382	0,0034	0,0626	0,8878	0,1342
P ROAD" "HUMBO	1,3568	0,4006	0,6272	0,6018	0,0531	0,025	0,4977	0,6604
LDT RID	-,	,,,,,,,	,,,,,	,,,,,,,,	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	,,,,,	3,1377	,,,,,,,
GE SOUT H"								
"FLOOK	1,185	0,6065	0,9691	0,8579	0,0168	0,0167	0,853	0,3232
BURN" "TRAINE	0,7952	0,4357	0,7335	0,6906	0,0154	0,0046	0,0283	0,5233
R PLAYA N2"								
"LONE P	0,9579	0,3861	0,5919	0,3265	0,2156	0,027	0,8645	0,9306
INE ROA D"								
"HOUSE	1,1206	0,4649	0,7693	0,5875	0,1435	0,0235	0,3488	0,8754
BUTTE N 4"								
"PRETT	1,3709	0,5139	0,7089	0,6132	0,0443	0,1594	0,6795	0,6081
Y ROCK RESERV								
OIR" "ROY RE	0,8993	0,5534	0,9383	0,7922	0,1126	0,0529	0,0564	0,7921
	-,-//-	0,0001	0,7505	,	J,1120	0,002/	0,0001	·,//=1

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SERVOI R"								
	0.001	0.2201	0.5100	0.5222	0.0016	0.000	0.2007	0.0125
"VIRTUE	0,921	0,3301	0,5133	0,5322	0,3316	0,0238	0,3097	0,9135
N2"								
"EAST W	0,7537	0,4044	0,5925	0,5001	0,2744	0,0368	0,4748	0,9414
IDMAN"								
"STICKY	0,8697	0,5194	0,8581	0,7147	0,2088	0,0243	0,141	0,709
JOE N1"								